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By BRUCE B. COLLETTE

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By Bruce B. Collette[1]

Introduction

Breeding tubercles are epidermal structures that function primarily in facilitating contact between individuals during spawning. Tubercles are used by some fishes to defend their nests and territories or to protect their body and fin surfaces in nest building. Breeding tubercles are present on species of at least 13 different families of fishes in three orders. Except in the Cyprinidae and Catostomidae, their presence either has been ignored or has been mentioned briefly, with little comment on their biological or systematic importance. The purpose of this study is to survey the Percidae for the presence of breeding tubercles and to compare the different tubercle patterns with the present classification of the family. This paper is the fourth in a series on the systematics of the Percidae (see Collette, 1962, 1963; Collette and Yerger, 1962). A review of the occurrence and significance of breeding tubercles in fishes is currently in preparation.

In view of the large number of reports of breeding tubercles in the Cyprinidae and the Catostomidae, it is somewhat surprising that they

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have been neglected in the Percidae. Only 13 papers, covering 16 species in 3 genera, report tubercles. I can now triple the number of species and add 2 genera. Jordan's (1877) description of the tubercles on *Percina evides* is the first such record for this family. From 1931 to 1958, tubercles were reported by Vladykov, 1931 (*Zingel streber*); Hubbs and Cannon, 1935 (*Etheostoma serriferum, E. gracile, E. fusiforme*); Bailey, 1948 (*Percina evides, P.* (*Imostoma*) species, *Etheostoma nianguae*); Moore and Cross, 1950 (*Etheostoma cragini*); Moore and Rigney, 1952 (*E. radiosum*); Cross, 1954 (*Percina shumardi, Etheostoma gracile*); Hubbs, 1954 (*Percina shumardi*); Cross and Minckley, 1958 (*Etheostoma stigmaeum*); Winn, 1958b (*E. stigmaeum, E. microperca*). In recent years, tubercles have been reported by Collette, 1962 (the six species of the subgenus *Hololepis*, adding *Etheostoma zoniferum, E. collis, E. saludae* to the three noted by Hubbs and Cannon, 1935); Distler and Metcalf, 1962 (*E. pallididorsum*); and Bailey and Richards, 1963 (*E. hopkinsi*).

Methods.—In order to find tuberculate material, or to ascertain that a given species is not tuberculate, it was necessary to examine large numbers of specimens. Particular attention was paid to collections made during the spring. Specimens were examined under a binocular microscope and compressed air was used to dry the scales and fin-rays to make the tubercles discernible. The presence of tubercles is ephemeral in many species; therefore the fact that I have not recorded them for a given species does not prove that they do not occur. Gonad development was frequently estimated and recorded, especially in cases where tubercles were not found. The descriptions of breeding tubercles of each species are based on the specimens with the best developed tubercles, although, when adequate collections were available, additional specimens were utilized to trace seasonal development. Catalog numbers, locality, and date of collection are given for at least the best tuberculate material examined of each species.

The study is based upon a survey of the percids in the collections of the U.S. National Museum (USNM), Cornell University (CU), University of Michigan Museum of Zoology (UMMZ), and Tulane University (TU), with additional observations on specimens from the Academy of Natural Sciences of Philadelphia (ANSP), Museum of Comparative Zoology (MCZ), University of Kansas (KU), Virginia Polytechnic Institute (VPI), University of Georgia (UG), University of Mississippi (UM), Illinois Natural History Survey (INHS), University of Texas (TNHC), University of Florida (UF), Florida State University (FSU), and Charles University, Prague. I have examined preserved males in breeding condition of at least 100 the approximately

118 species of Percidae. I also examined nonbreeding material of all species except *Stizostedion marinum*.

Tubercle patterns, together with brief comments on other types of sexual dimorphism, are described, species by species, in the following sections. The suprageneric classification used follows that outlined in a recent paper (Collette, 1963), where the Percidae was divided into two subfamilies, the Luciopercinae and the Percinae. Each of these subfamilies was subdivided into two tribes, the Luciopercini and the Romanichthyini in the first subfamily, and the Percini and Etheostomatini in the second. The arrangement of genera, subgenera, and species within the Etheostomatini (table 1) is modified from that presented by Bailey (*in* Bailey and Gosline, 1955).

For the loan of specimens and other assistance, I wish to thank Edward C. Raney, Cornell University; Robert H. Gibbs, Jr., Ernest A. Lachner, and W. Ralph Taylor, U.S. National Museum; Reeve M. Bailey, University of Michigan; Royal D. Suttkus, Tulane University; Frank B. Cross, University of Kansas; James E. Böhlke, Philadelphia Academy of Natural Sciences; Clark Hubbs, University of Texas; Ota Oliva, Charles University, Prague; Giles W. Mead, Museum of Comparative Zoology, Harvard University; Y. J. McGaha, University of Mississippi; and Robert R. Ross, Virginia Polytechnic Institute. Petru Bănărescu of the Academia Republicii Populare Romine deserves extra thanks for sending specimens of all the Rumanian percids to the museums of the United States. To Robert V. Miller, Rudolph J. Miller, Leslie W. Knapp, and William J. Richards, I owe a special debt of gratitude for their efforts in providing me with data and material on percid breeding tubercles. Without the help of this group of former fellow Cornell students, my work would have been immeasurably more difficult. Mildred H. Carrington has drawn the figures which valuably supplement this paper. Reeve M. Bailey, Daniel M. Cohen, Robert H. Gibbs, Jr., Ernest A. Lachner, and Rudolph J. Miller have all offered valuable suggestions on the manuscript.

Tribe Luciopercini

Genus *Stizostedion* Rafinesque

There is little sexual dimorphism in the five species of *Stizostedion*—*canadense* (Smith), *lucioperca* (Linnaeus), *marinum* (Linnaeus), *vitreum* (Mitchill), and *volgense* (Gmelin)—and breeding tubercles are apparently absent. Females of all species reach a larger maximum size than the males and on the average are longer and heavier in a given year class, at least after the first two years of life. For *S. canadense*, see Carlander (1950); for *S. vitreum* see Eschmeyer (1950), Hile (1954)

TABLE 1.—*Distribution of breeding tubercles in the fishes of the family Percidae* (+ = present; 0 = absent; ? = material not adequate; ♂ and ♀ are placed under areas where tubercles were found: TP? = tubercles present?; Bd = body; A = anal fin; P_2 = pelvic fins; C = caudal fin; Hd = head; Ch = chin; P_1 = pectoral fins; D = dorsal fins; Br = branchiostegals)

Taxon	TP?	Bd	A	P_2	C	Hd	Ch	P_1	D	Br
Luciopercini										
Stizostedion	0	–	–	–	–	–	–	–	–	–
Romanichthyini										
Zingel										
asper	+?	–	–	–	–	–	–	–	–	–
streber	+	♂ ♀	–	–	–	♂ ♀	–	♂ ♀	–	–
zingel	+	♂ ♀	–	–	–	♂ ♀	–	♂ ♀	♂	–
Romanichthys										
valsanicola	+	♂ ♀	♂	♂ ♀	♂ ♀	♂	–	♂ ♀	♂	–
Percini										
Perca	0	–	–	–	–	–	–	–	–	–
Gymnocephalus	0	–	–	–	–	–	–	–	–	–
Percarina	0?	–	–	–	–	–	–	–	–	–
Etheostomatini										
Percina										
(*Hypohomus*)	0	–	–	–	–	–	–	–	–	–
(*Alvordius*)	0	–	–	–	–	–	–	–	–	–
(*Hadropterus*)	0	–	–	–	–	–	–	–	–	–
(*Swainia*)	0	–	–	–	–	–	–	–	–	–
(*Percina*)										
caprodes	+	♂	–	–	–	–	–	–	–	–
rex	+	♂	–	–	–	–	–	–	–	–
(*Ericosma*)										
palmaris	0	–	–	–	–	–	–	–	–	–
crassa	0	–	–	–	–	–	–	–	–	–
evides	+	♂	♂	♂	♂	♂	♂	–	–	♂
(*Imostoma*)										
shumardi	+	♂	♂	♂	♂	♂	–	–	–	–
uranidea	+	♂	♂	♂	♂	♂	–	♂	–	–
(*Cottogaster*)	0	–	–	–	–	–	–	–	–	–
Ammocrypta										
(*Crystallaria*)										
asprella	+	–	♂	♂	–	–	–	–	–	–
(*Ammocrypta*)										
vivax	+	–	♂	♂	–	–	–	–	–	–
pellucida	+	–	–	♂	–	–	–	–	–	–
clara	+	–	♂	♂	♂	–	–	–	–	–
beanii	+	–	♂	♂	–	–	–	–	–	–
Etheostoma										
(*Boleosoma*)										
nigrum	0	–	–	–	–	–	–	–	–	–
olmstedi	0	–	–	–	–	–	–	–	–	–
perlongum	0	–	–	–	–	–	–	–	–	–
longimaeum	0	–	–	–	–	–	–	–	–	–
podostemone	0	–	–	–	–	–	–	–	–	–
chlorosomum	+	–	♂	♂	–	–	–	–	–	–
stigmaeum	+	♂	♂	♂	–	–	–	–	–	–
jessiae	+	♂	♂	♂	–	–	–	–	–	–
(*Ioa*)	0	–	–	–	–	–	–	–	–	–
(*Etheostoma*)										
variatum	+	♂ ♀	–	–	–	–	–	–	–	–
tetrazonum	+	♂ ♀	–	–	–	–	–	–	–	–
euzonum	+	♂ ♀	–	–	–	–	–	–	–	–

TABLE 1.—Continued

Taxon	TP?	Bd	A	P_2	C	Hd	Ch	P_1	D	Br
Etheostomatini—Continued										
Etheostoma—Continued										
(*Etheostoma*)—Continued										
kanawhae	+	♂ ♀	–	–	–	–	–	–	–	–
osburni	+	♂ ♀	–	–	–	–	–	–	–	–
inscriptum	+	♂	–	–	–	–	–	–	–	–
thalassinum	+	♂	–	–	–	–	–	–	–	–
swannanoa	+	♂	–	–	–	–	–	–	–	–
blennioides	+	♂	–	–	–	–	–	–	–	–
gutselli	+	♂	–	–	–	–	–	–	–	–
blennius	0?	–	–	–	–	–	–	–	–	–
sellare	0?	–	–	–	–	–	–	–	–	–
rupestre	0	–	–	–	–	–	–	–	–	–
histrio	0	–	–	–	–	–	–	–	–	–
zonale	0	–	–	–	–	–	–	–	–	–
(*Ulocentra*)	0	–	–	–	–	–	–	–	–	–
(*Allohistium*)	0	–	–	–	–	–	–	–	–	–
(*Nothonotus*)	0	–	–	–	–	–	–	–	–	–
(*Oligocephalus*)										
nianguae	+	♂	–	–	–	–	–	–	–	–
sagitta	+	♂	–	–	–	–	–	–	–	–
radiosum	+	♂	–	–	–	–	–	–	–	–
whipplii	+	♂	–	–	–	–	–	–	–	–
caeruleum	+	♂	–	–	–	–	–	–	–	–
punctulatum	+	♂	♂	♂	♂	–	–	–	–	–
parvipinne	+	–	♂	–	–	–	–	–	–	–
fricksium	+	–	♂	–	–	–	–	–	–	–
hopkinsi	+	♂	♂	♂	–	–	–	–	–	–
spectabile	+	♂	♂	♂	♂	–	–	♂	–	–
luteovinctum	+	♂	♂	♂	♂	–	–	–	–	–
cragini	+	♂	♂	♂	–	–	–	–	–	–
pallididorsum	+	♂	♂	♂	–	–	–	–	–	–
asprigene	0	–	–	–	–	–	–	–	–	–
swaini	0	–	–	–	–	–	–	–	–	–
mariae	0	–	–	–	–	–	–	–	–	–
juliae	0	–	–	–	–	–	–	–	–	–
pottsii	0	–	–	–	–	–	–	–	–	–
lepidum	0	–	–	–	–	–	–	–	–	–
exile	0	–	–	–	–	–	–	–	–	–
grahami	0	–	–	–	–	–	–	–	–	–
(*Villora*)	0	–	–	–	–	–	–	–	–	–
(*Austroperca*)	?	–	–	–	–	–	–	–	–	–
(*Psychromaster*)	0	–	–	–	–	–	–	–	–	–
(*Catonotus*)	0	–	–	–	–	–	–	–	–	–
(*Hololepis*)										
serriferum	+	–	♂	♂	–	–	–	–	–	–
gracile	+	–	♂	♂	–	–	♂	–	–	–
zoniferum	+	–	♂	♂	–	–	♂	–	–	–
fusiforme	+	–	♂	♂	–	–	–	–	–	–
saludae	+	–	♂	♂	–	–	–	–	–	–
collis	+	–	♂	♂	–	–	–	–	–	–
(*Microperca*)										
proeliare	+	–	♂	♂	–	–	–	–	–	–
microperca	+	–	♂	♂	–	–	–	–	–	–
fonticola	+	–	♂	♂	–	–	–	–	–	–

and Rawson (1957); and for the three European species, see data presented by Berg (1949). Vladykov (1931) and Oliva (1953) reported that males of *S. lucioperca* have relatively longer fins than the females. Vladykov (1931) noted the same for *S. volgense*.

Tribe Romanichthyini

Genus *Zingel* Cloquet

There are three species in this genus: *asper* (Linnaeus), *streber* (Siebold), and *zingel* (Linnaeus). Both sexes of *Z. streber* and *Z. zingel* are tuberculate; *Z. asper* also will probably be found to be so.

I have examined 10 tuberculate males of *Zingel streber* (ANSP 82497, Rumania, Mures R., 108 mm.; USNM 187742, Rumania, Criscul R., 57–108 mm.; and USNM 190212, Rumania, Timis R., 98–99 mm.), all collected in October, and 9 tuberculate females from the same collections, plus USNM 187740 (Criscul R., April, 131 mm.). In the male, where they are best developed (USNM 190212, 99 mm.), tubercles are present on all the head scales including those on the opercle and preopercle. These tubercles are elongated longitudinally with the point of the tubercle projecting upward and posteriorly beyond the margin of the scale. A few head scales have two tubercles per scale, but the majority only have one. Prominent ridgelike tubercles are developed on all the body scales above the lateral line posterior as far as the middle of the caudal peduncle. They are also present on several rows of scales below the lateral line in the region posterior to the tip of the pectoral fin. The females and the other males have a similar pattern of tubercle development, but the tubercles are more ridgelike and less prominent and are not on as many scales. The individual tubercles are aligned in the same direction from one scale to the next, creating continuous ridges along the body. Among the Percidae, this condition is unique in the genus *Zingel*. None of the tuberculate specimens show any sign of tubercles on any of the fins. Rudolph J. Miller examined a 150 mm. gravid tuberculate female of *Z. streber* (Charles University No. 9908, Czechoslovakia, Orawa R., April 4) and he corroborates what I have found, although the tubercles seem to have been somewhat better developed than in the females I examined. Vladykov (1931) reported that *Zingel streber* had tubercles on the pectoral fins as well as on the head and the body.

I have examined one tuberculate specimen of *Zingel zingel*, a 175 mm. male that Dr. Miller found for me (Charles University no. 4514, Czechoslovakia, Danube R., May 5). There are tubercles on all the head scales and on the dorsal and dorsolateral body scales. These tubercles are only slightly raised and do not form longitudinal rows as they do in *Z. streber*. There are tubercles on the anterior ten rays in

the second dorsal fin and on the anterior surface of the upper pectoral rays. None are present on the first dorsal, anal, or pelvic fins. Two other males with greatly enlarged testes (MCZ 3063) and 7 egg-filled females (USNM, MCZ, ANSP) lack tubercles. Dr. Miller also examined a large female *Z. zingel* in the Charles University collection which had poorly developed tubercles on the head scales, scales of the anterior dorsum, and on the pectoral rays. Vladykov (1931) reported that sexual dimorphism was rather marked in this species, but only mentioned that the paired fins of the males were much longer than those of the females.

I examined one male of *Zingel asper* with well-developed testes (ANSP 14055, France, Rhone R., 116 mm.) and one female filled with large eggs (MCZ 2551, Saone R., 105 mm.). Neither had any breeding tubercles. Both specimens, however, were in poor condition, and *Z. asper* will probably be found to have a tubercle distribution very similar to that of its close relative *Z. streber*.

Genus *Romanichthys* Dumitrescu, Bănărescu, and Stoica

I have examined four tuberculate males of the only species in this genus, *Romanichthys valsanicola* Dumitrescu, Bănărescu, and Stoica (USNM 190149, Arges R., May 22, 66 mm.; USNM 187749, Arges R., May–June, 68 mm.; MCZ 40966, Vilsan R., June–Aug., 85 mm.; and UMMZ uncat., Arges R., June–July, 76 mm.) and two tuberculate

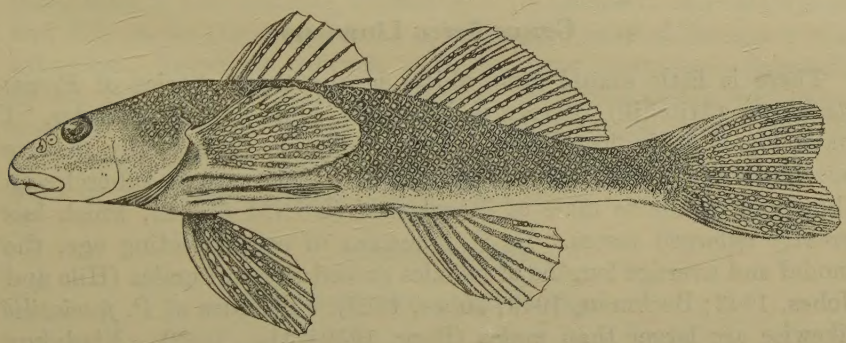

FIGURE 1.—Male of *Romanichthys valsanicola* showing the distribution of breeding tubercles (USNM 190149, Rumania, Arges River, May 22, 66 mm. SL).

females (MCZ 40966, 86 mm. and UMMZ uncat., 69 mm.). Another male (USNM 190180, 92 mm., June–Aug.) has well-developed testes but lacks tubercles. Four females (USNM 190149, 96 mm.; MCZ 40966, 80 and 89 mm.; and UMMZ uncat., Vilsan R., Oct. 19, 65 mm.) also lack tubercles. The tubercles are best developed in the smaller USNM male (fig. 1). There are a few small tubercles distally on the dorsal surface of pelvic soft rays 2–5 and ventrally on rays 3–5.

Tubercles are present along the outside of the pectoral fin on the upper 10–11 rays and on the inside on the lower 2–6 rays. The tubercles on the outer surface are longer and relatively low; those on the inner surface are smaller and more conical. Tubercles are present on the upper principal caudal rays, on the dorsal 3–4 rays of the lower half of the caudal fin, and on the last three anal soft rays. Tubercles are developed distally on all but the first two dorsal spines and on the entire length of the second dorsal rays. This is the only percid with tubercles on both dorsal fins. A low conical tubercle is present in the center of most of the exposed body scales, although the tubercles are smaller on the ventral side of the caudal peduncle. Tubercles also are present on the dorsal half of the opercle. In many ways, the overall appearance of the body tubercles on this specimen is reminiscent of the tubercle pattern of the minnow *Campostoma anomalum* (see color plate, Forbes and Richardson, 1909). One tuberculate female of *R. valsanicola* (MCZ 40966) has small tubercles on many of the body scales, the distal parts of the pectoral rays, the distal tip of pelvic soft ray 4 (dorsal surface), and a few scattered tubercles on the upper caudal fin rays. Another (UMMZ uncat.) has only a few poorly developed tubercles on the pectoral rays. In the lengthy original description of this genus and species (Dumitrescu, Bănărescu, and Stoica, 1957) there was no mention of breeding tubercles.

Tribe Percini

Genus *Perca* Linnaeus

There is little sexual dimorphism in the three species of *Perca: flavescens* (Mitchill), *fluviatilis* Linnaeus, and *schrenki* Kessler. I have found no indication of breeding tubercles in sexually mature specimens of *P. flavescens* or P. *fluviatilis*. There are no tubercles on the single available male of *P. schrenki* (USNM 55712), which has greatly enlarged testes. In *P. flavescens* of corresponding age, the modal and average lengths of females exceed those of males (Hile and Jobes, 1942; Beckman, 1949; Jobes, 1952). Females of *P. fluviatilis* likewise are larger than males (Berg, 1949; Alm, 1952). Vladykov (1931) and Oliva (1953) found that the paired fins of *P. fluviatilis* are longer in males than in females.

Genus *Gymnocephalus* Bloch

There is sexual dimorphism in *Gymnocephalus*. Males of *G. cernua* (Linnaeus) and *G. schraetser* (Linnaeus) are smaller than females (Vladykov, 1931; Oliva, 1953) and the paired fins of the males are somewhat longer. There are no tubercles on nine males of

Gymnocephalus cernua (USNM, UMMZ; 60–87 mm.) with greatly enlarged testes or on 20 egg-filled females (68–158 mm.) from these and nine other USNM collections. Tubercles are absent from five males of *G. schraetser* (ANSP, UMMZ, USNM; 92–117 mm.) with greatly enlarged testes and from nine egg-filled females (105–155 mm.). Smitt (1892, p. 42) reported that there was little external distinction between males and females of *Gymnocephalus acerina* (Güldenstädt). He found that males had longer pelvic fins and deeper bodies than females, but he did not mention breeding tubercles. The one specimen available to me (USNM 28564) is an egg-filled female lacking tubercles.

Genus *Percarina* Nordmann

I have examined three specimens of *Percarina demidoffi* Nordmann (USNM 37308 and MCZ 26527). All are females filled with eggs. All lack tubercles.

Tribe Etheostomatini

The darter tribe is the most speciose in the family, with 102 valid described species, plus about a dozen undescribed ones. Bailey (*in* Bailey, Winn, and Smith, 1954; and *in* Bailey and Gosline, 1955) has recently reduced the nominal genera of darters to three: *Percina* (22 species in 8 subgenera), *Ammocrypta* (5 species in two subgenera), and *Etheostoma* (76 species in 13 subgenera). Several changes within subgenera, based on tubercle patterns, seem necessary, especially in the subgenera *Ericosma*, *Boleosoma*, *Ioa*, *Etheostoma*, and *Oligocephalus*. I hesitate to make nomenclatorial changes based primarily on breeding tubercle patterns, and in this paper I shall merely discuss some of the groups in which reallocation seems desirable.

Genus *Percina*

Subgenus *Hypohomus* Cope

This subgenus contains three species: *aurantiaca* (Cope), *cymatotaenia* (Gilbert and Meek), and one undescribed species. Males apparently lack breeding tubercles, although a unique adaptation probably performs the same function. Bailey (1948) pointed out that males of *Hypohomus* have a thin flangelike midventral keel on the lower edge of the caudal peduncle near the caudal base bearing strongly developed ctenoid scales. This seems especially significant, because males of the subgenus *Hypohomus* have the fewest enlarged midventral scales of any of the subgenera of *Percina*. It will be interesting to see how these keels function in spawning.

Males of *P. aurantiaca* in 7 collections (UMMZ, USNM), taken from April 19 through October 3, lack tubercles. One of these specimens, a 132 mm. male taken April 29 (UMMZ 129572, Tennessee, Little Pigeon R.), has greatly enlarged testes and appears to be near spawning condition. No males of *P. cymatotaenia* collected in the spring were examined, but a 69 mm. male taken on August 26 (UMMZ 152290, Mo., Gasconade R.) has slightly enlarged testes and a well-developed caudal keel. The ventral scales of this specimen have well developed ctenii, making the venter very rough to the touch. The best-developed caudal keels I have observed were pointed out to me by Reeve M. Bailey and are in three males of the undescribed species of *Hypohomus* (UMMZ 165304, Kentucky, Green R., April 5, 50–65 mm.). They are covered with ctenoid scales resembling the modified midventral scales usually present in males of *Percina*. The anal fin of these males, considerably longer than that of the two females in the same collection, reaches to the base of the caudal, thus connecting it with the caudal keel and apparently forming a single functional unit.

Subgenus *Alvordius* Girard

There are five species in this subgenus: *macrocephala* (Cope), *maculata* (Girard), *notogramma* (Raney and Hubbs), *pantherina* (Moore and Reeves), and *peltata* (Stauffer). I have examined adequate breeding material of the last four species and have found no tubercles. Males have enlarged midventral scales and considerably more pigment in the first dorsal fin than the females have. Both sexes of *P. maculata* are equal in size. The males lack breeding tubercles, but the genital papillae of the females are elongate, broad, and tube-like (Winn, 1958b, p. 172). Petravicz (1938) did not mention breeding tubercles in this species. *P. maculata* spawns over sand or gravel, with the male mounted on the female's back (Winn, 1958b, fig. 4). *P. peltata* spawns in a similar manner, but the male's caudal peduncle does not lie alongside the female's, as is the case of most darters. The enlarged caducus scales on the male belly apparently serve both to stimulate the female and to enable the male to maintain his position over her (New, 1963; and pers. comm.).

Subgenus *Hadropterus* Agassiz

There are three described species in this subgenus: *nigrofasciata* (Agassiz), *sciera* (Swain), and *lenticula* Richards and Knapp. There are no tubercles on specimens taken in six March–April collections of *P. nigrofasciata* from Georgia, Alabama, and Mississippi. The ovaries and testes of these specimens are greatly enlarged, indicating

that they are close to spawning condition. Several of the males are extremely darkly pigmented. Crawford (1956) thus describes sexual dimorphism in *P. n. nigrofasciata:* The males are larger and darker than females; the vertical bars of the males tend to be more discrete and less confluent; enlarged ctenoid scales are present along the midventral line on the males' bellies; and the genital papillae in the females are long, conical, and clearly villiform.

No tubercles are present on specimens of *P. sciera* in three Oklahoma–Texas collections taken in March and April. The testes and ovaries of all these specimens are greatly enlarged. The vertical banding present in the females becomes completely obscured by the dark pigment in breeding males. The fins, belly, and breast are almost black in these males. Males have enlarged scales along the midventral line of their bellies.

There are no tubercles on the two males of the recently described *P. lenticula* collected in the spring (CU 43592, Alabama drainage, May 9, 96 mm., holotype; CU 43594, Alabama drainage, May 17, 86 mm., paratype). There is little sexual dimorphism in color pattern (Richards and Knapp, 1963).

Subgenus *Swainia* Jordan and Evermann

There are four species in this subgenus: *nasuta* (Bailey), *oxyrhyncha* (Hubbs and Raney), *phoxocephala* (Nelson), and *squamata* (Gilbert and Swain). I have examined 15 collections of *P. phoxocephala* taken from mid-March to September (UMMZ, USNM, KU), a male of *oxyrhyncha* taken on June 25 (UMMZ 118422, holotype), a male of *squamata* taken on May 25 (UMMZ 177816), and 5 males of *nasuta* taken on April 26 (CU 41971), and have found no tubercles. Trautman (1957, p. 543) reported that breeding males of *P. phoxocephala* are more intensely colored than females and have orange bands on the first dorsal fin.

Subgenus *Percina* Haldeman

There are two species in this subgenus: *caprodes* (Rafinesque), with several subspecies, and *rex* (Jordan and Evermann). Tubercles are present on the ventral scale rows of the males of both species. Tubercles seem to be better developed and present for a longer period in southern populations, *Percina caprodes carbonaria* (Baird and Girard), than in northern ones. Both species have low rounded tubercles on the posterior part of the scales. The tubercles are usually not prominent, so that magnification and drying are necessary to trace their extent. No fin tubercles were found, and the females lack tubercles altogether.

Specimens with tubercles of *P. caprodes carbonaria* have been found in five collections, dating from April 14 (CU 32822, Missouri, Lamine R.) to May 18 (TU 15493, Arkansas, Arkansas R.). Tubercles were found on males of *P. c. caprodes* × *P. c. semifasciata* (DeKay) intergrades taken April 20 (CU 8238, Pennsylvania, Shenango R., 88–110 mm. standard length). A male *P. caprodes* with well-developed tubercles (TU 15493, 102 mm.) had tubercles on the modified midventral scales, 5 rows on each side of the modified midventral row, 8 rows per side just anterior to the genital papilla, 4 rows along each side of the anal fin base, and 11 ventral caudal peduncle rows. The pelvic and anal fins and the venter of females lack pigment; these areas are darkened in males. Winn (1958b, p. 172) reported that both sexes of Michigan *P. caprodes* were of equal size, that the anal fins of males were larger than those of females, and that breeding tubercles were absent.

In spawning, the female *P. caprodes* stops over sand or gravel ahead of a male. The male swims up and mounts her with his pelvic fins over her relaxed first dorsal fin and his tuberculate lower sides in contact with her sides (Reighard, 1913; Winn, 1958a; 1958b, fig. 4). Sometimes accessory males vibrate with the spawning pair (Winn, 1958a).

One tuberculate male of *Percina rex* was examined (CU 16910, Virginia, Roanoke R., March 27, 105 mm.). It has tubercles on 2–3 rows of scales on each side of the midventral row and on the posterior ventral portion of the caudal peduncle. A female and a smaller male from this collection lack tubercles.

Subgenus *Ericosma* Jordan and Copeland

Three species are presently placed in this subgenus: *evides* (Jordan and Copeland), *crassa* (Jordan and Brayton), and *palmaris* (Bailey). The two latter species apparently lack tubercles, but males of *P. evides* have well-developed tubercles on numerous parts of the body (fig. 2). Jordan's (1877) discovery of tubercles on the pelvic and anal fins of *P. evides* was the first record of tubercles in the Percidae. Bailey (1948) also noted tubercles on the lower fins of this species.

Tubercles are present on males of *P. evides* in several collections taken from March 10 (UMMZ 103459, Tennessee, Clinch R.) to June 29 (UMMZ 131458, North Carolina, Swain Co.). Tubercles are present on the ventral surfaces of all pelvic soft rays (but apparently are absent from the spine), dorsally on the distal parts of pelvic soft rays 1–3, and laterally on the anal spines and soft rays. The tubercles are quite small and conical and, lacking pigment, stand out in contrast to the darkly pigmented fins. In males with

maximum tubercle development (CU 38055 and CU 38127, Georgia, Toccoa R., June 7) tubercles are present on most ventral scale rows posterior to the pelvic fins and below the lateral line. A few tubercles are present on some of the lateral line scales. The modified midventral scales have up to three tubercles per scale. This, with *P. uranidea* and *P. caprodes*, is one of the few darters in which tubercles are present on these scales and is the only species in which there is more than one tubercle per scale. If the midventral scales function in a manner analagous to the breeding tubercles, the possession of both tubercles and the modified scales seems unnecessary. It will

FIGURE 2.—Male of *Percina* (*Ericosma*) *evides* showing the distribution of breeding tubercles (USNM 44433, Indiana, Tippecanoe River, May 16, 53 mm. SL).

be interesting to learn how these structures function in the courtship-spawning act. Tubercles are present on some rays of the ventral half of the caudal fin. The cephalic pores of the preoperculomandibular and infraorbital canals are sites for small tubercles. These tubercles extend onto the chin beside the pores of the anterior portion of the preoperculomandibular canal, as in *Etheostoma* (*Hololepis*) *gracile* and *E.* (*H.*) *zoniferum*. Tubercles are present on some of the branchiostegal rays, a condition unique among the Percidae, although known for some Cyprinidae. Small scattered tubercles are present on parts of the opercle.

Among the Percinae, only *Percina* (*Imostoma*) *uranidea* has a tubercle distribution which approaches that of *P. evides*. *Romanichthys* and *Zingel* in the Lucioperciinae have large numbers of tubercles on the head, concentrated on top.

Tubercles are absent on specimens of *P. crassa* in several March and April collections (UMMZ), although the males have greatly enlarged testes and the females are filled with large eggs. Eight males of *P. palmaris* taken on March 31 (CU 17328, Georgia, Talking Rock Cr.) appear to be in full breeding color, but they lack breeding tubercles, although fleshy ridges similar to those in *Etheostoma*

(*Oligocephalus*) *nianguae* are well developed on the anal elements and, to a lesser degree, on the ventral surfaces of the pelvic rays. Lack of tubercles may indicate that these two species are not as closely related to *P. evides* as was indicated by Bailey (1940; and *in* Bailey and Gosline, 1955).

Subgenus *Imostoma* Jordan

There are two species in this subgenus: *shumardi* (Girard) and *uranidea* (Jordan and Gilbert). Males of both species have tubercles on many areas and have the anal fin greatly elongated so that it reaches to the caudal base. Bailey (1948) reported tubercles on the lower fins of "the several species" of *Imostoma*.

Tubercles are present on males of *P. shumardi* taken from January 12 (TU 14902, Mississippi, Pearl R.) to July 7 (USNM 44432, Indiana, Wabash R.). At maximum development (USNM 187775, Texas, Guadalupe R., Feb. 4, 47–56 mm.; UMMZ 81563, Michigan, Au Sable R., April 30, 38–45 mm.; and KU 3208, Kansas, Neosho R., April 10, 49–51 mm.) large high tubercles are present on the entire length of the anal soft rays. Small tubercles are present on the second anal spine. Tubercles are present on the entire length of the ventral surface of pelvic soft rays 1–2 or 2–3 and on the distal tip of rays 3–4. Tubercles cover the entire length of the most ventral five principal rays of the caudal fin and a few are found on the distal tips of the next two rays. Cross (1954) reported tubercles on the anal and caudal fins of the KU specimens. In a 55 mm. male from USNM 187775, a small tubercle is also present on the posterior portion of each of the midventral scales, in addition to a few tubercles above the upper jaw next to the openings of the infraorbital canal and a few scattered tubercles on the posterior portions of the preopercle and opercle. Tubercles are better developed on larger males as shown by TU 14902, in which three males, 59–67 mm. long, lack tubercles and three males, 62–70 mm., have well-developed tubercles. Hubbs (1954) has noted elongate tubercles on the anal rays of mature males.

P. uranidea is even more tuberculate than *P. shumardi*, and is exceeded in the Percidae only by *Romanichthys valsanicola* and *P.* (*Ericosma*) *evides*. At maximum tubercle development, males have tubercles on almost all surfaces of the ventral half of the body (fig. 3). The tubercles on the anal fin closely resemble those on *P. shumardi* and are found at maximum development on the distal half to three-fourths of all anal soft rays. Similar tubercles are present on the ventral surface of all the elements of the pelvic fin, but they are larger and better developed on the soft rays than on the spine. Although they are also present on the dorsal surface, they are less numerous

and tend to be confined to the distal portion of the soft rays. Tubercles sometimes are developed on the few imbedded breast scales, the modified midventral scales, many of the scale rows lateral to the midventral rows, and on the ventral rows of caudal peduncle scales. As in *P. shumardi* and *P. evides*, small tubercles develop near the pores

FIGURE 3.—Male of *Percina* (*Imostoma*) *uranidea* showing the distribution of breeding tubercles (TU 7965, Louisiana, Pearl River, Feb. 16, 50 mm. SL).

of the infraorbital and preoperculomandibular canals. Small tubercles are present along some of the rays of the ventral half of the caudal fin. A few specimens have tubercles developed on the ventral 2–5 rays of the pectoral fin, a condition found only in one other species of the Etheostomatini, *Etheostoma* (*Oligocephalus*) *spectabile*.

The abundant material of *P. uranidea* in the Tulane University collections taken throughout the year from Pearl River makes a study of the annual development of the breeding tubercles possible. Maximum development occurs from February 8–16 (table 2), when the peak of spawning most likely occurs.

TABLE 2.—*Development of breeding tubercles in males of* Percina (Imostoma) uranidea *from the Pearl River* (see table 1 for abbreviations; L. Caud.=lower caudal fin)

Dates	Tubercle distribution					
	A	P_2	L. caud.	Bd	P_1	Hd
November 3	–	–	–	–	–	–
December 8	+	+	–	–	–	–
January 28	+	+	–	–	–	–
February 3	+	+	+	–	–	–
February 8–16	+	+	+	+	+	+
March 9	+	+	+	+	–	–
March 28	+	+	+	–	–	–
April 3	+	+	–	–	–	–
April 10	+	+	–	–	–	–
May 8	–	–	–	–	–	–
May 23	–	–	–	–	–	–

Subgenus *Cottogaster* Putnam

P. copelandi (Jordan) is the only known species. I have examined three large collections (USNM) from June, July, and August, an April collection from Pearl River (TU 17732), and several additional collections taken from February through July (UMMZ), and have found no tubercles. The ovaries and testes of these specimens are greatly enlarged. Males have melanophores concentrated in the center of each of the membranes of the first dorsal fin; they have much darker pelvic fins and somewhat darker second dorsal and anal fins, belly, and breast, than the females. Males have 5–12 enlarged mid-ventral scales. Winn (1953, 1958b) reported that males were larger and more heavily pigmented than females, had larger anal fins, and lacked breeding tubercles. The genital papilla of the breeding female is elongate and tubelike. *P. copelandi* spawns over gravel with the male mounted on the female's back (Winn, 1953; 1958b, fig. 4).

Genus *Ammocrypta* Jordan

This genus contains two subgenera: *Crystallaria* Jordan and Gilbert, with a single species, *asprella* (Jordan), and *Ammocrypta* Jordan, with four species, *vivax* Hay, *pellucida* (Agassiz), *clara* (Jordan and Meek), and *beanii* Jordan. Males of all five species probably will be found to have tubercles on the rays of the anal and pelvic fins, confirming the synonymizing of *Crystallaria* under *Ammocrypta* on the basis of tubercle distribution.

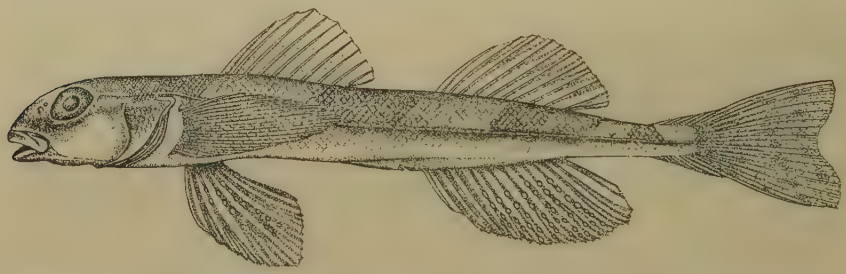

FIGURE 4.—Male of *Ammocrypta* (*Crystallaria*) *asprella* showing the distribution of breeding tubercles (USNM 172363, Louisiana, Ouachita River, Jan. 28, 75 mm. SL).

Tubercles on *A. asprella* begin to develop by late November (TU 1851, Mississippi, Pearl R.), when they are noticeable on the anal spine and the first nine anal soft rays. The maximum development (fig. 4) I have found occurs in the latter half of January (TU 7536, 14921, 15174; Mississippi, Pearl R.; USNM 172363, Louisiana, Ouachita R.). Large conical tubercles are developed on the spine and all the anal soft rays except the last 1–3. In these specimens tubercles are present only on the ventral surface of pelvic soft rays

3–5, but they may be found on the other pelvic fin elements when more material (probably February specimens) is examined.

Males of *A. beanii* develop tubercles on the ventral surface of the pelvic spine and on soft rays 1–4 by March 9 (TU 3843, Louisiana, Pearl R.). By April 26 (TU 19992, Mississippi, Homochitto R.), much larger tubercles are present on the ventral surface of all the pelvic elements and on the distal eighth to two-thirds of all the anal soft rays, but not on the anal spine. A few tubercles are present distally on the dorsal surface of pelvic soft rays 1–3. A male taken on August 17 (TU 24061, Florida, Yellow R.) also has this tubercle distribution, but the tubercles are smaller.

Breeding tubercles are present on males of *A. clara* from as early as June 20 (UMMZ 127887, Arkansas, Saline R., 32–35 mm.) until July 28 (UMMZ 148570, Missouri, Salt R., 38–43 mm.). At the maximum development I have seen (UMMZ 148570), small tubercles are present on the entire length of the ventral surface of the pelvic spine and soft rays. Similar tubercles are present on the distal half to three-fourths of the anal soft rays, but none are developed on the spine. The ventralmost two primary caudal rays have tubercles.

A tubercle distribution similar to that of *A. beanii* was found on males of *A. vivax* taken May 13 (USNM 172539, Louisiana, Red R.) and July 29 (USNM 172557, Louisiana, Red R.).

Tubercles were present on the pelvic rays of males of *A. pellucida* in three collections (UMMZ 100864, Indiana, Salomonie R., May 31; UMMZ 107758, Ohio, Salt Cr., June 8; CU 32967, Ohio, Big Darby Cr., Aug. 22). Additional material will probably show the presence of tubercles on the anal fin also.

Genus *Etheostoma*

Subgenus *Boleosoma* DeKay

This subgenus can be divided into two or three species groups. The *nigrum* group includes five species: *nigrum* Rafinesque, *longimanum* Jordan, *olmstedi* Storer, *perlongum* (Hubbs and Raney), and *podostemone* Jordan and Jenkins. Breeding tubercles do not develop in these species, the tips of the pelvic spines become swollen during the breeding season, and the males have only brown and black pigmentation. These species have a complex spawning behavior under rocks. The second group is comprised of two closely related species: *E. stigmaeum* (Jordan) and *E. jessiae* (Jordan and Brayton). Males of both of these species develop breeding tubercles on the pelvic and anal fins. In addition, they also have tubercles on the ventral scale rows as in the *E.* (*Etheostoma*) *variatum* species group. Males are brightly colored during the breeding season. *E. stigmaeum*

spawns with the male mounted on the female's back like most darters. The third group includes *E. chlorosomum* (Hay), males of which have tubercles on the pelvic and anal fin rays only. Thus, on these criteria, the subgenus *Boleosoma* is not a natural group. In some respects the *nigrum* group is closer to the subgenus *Ioa* than to the *stigmaeum* group, although *E. chlorosomum* is somewhat intermediate between the two groups of *Boleosoma*.

Cole (1957) noted that, as the spawning season for *E. nigrum nigrum* approached, the body became blackened; the W and X lateral markings became darker and appeared as diffuse blotches; the dorsal saddles became less pronounced; the head and lips became black; lines and spots on much of the body tended to disappear; the pelvic and anal elements became heavily blackened and the membranes became only slightly less blackened; the pectoral, dorsals, and caudal darkened; the pelvic spine and the first two or three rays and the more ventral elements of the pectoral fin acquired whitened knoblike tips. This tendency is shown to an extreme degree by one of Cole's (1957) undescribed subspecies of *E. nigrum*, in which the lower pectoral membranes became separated at the tips of the rays in the breeding males and females and ended in large, fleshy, whitish knobs. These knobs apparently serve to protect the tips of the rays during spawning and nest defense. Winn (1958b, p. 172) reported that males of *E. nigrum nigrum* were larger than females and had larger anal, first dorsal, second dorsal, pectoral, and pelvic fins, and had the first four or five spines of the first dorsal fin adorned with thickened, opaque, white tips. *E. n. nigrum* spawns upside down underneath rocks and the male subsequently defends the nest (Winn, 1958a; 1958b, fig. 5).

Breeding males of *E. olmstedi* also become very dark but not to so extreme a degree as in *E. nigrum* (Cole, 1957). *E. olmstedi* breeds in a similar manner to *E. nigrum* (Atz, 1940). Males of *E. longimanum* taken in April and June differ from females in having the pigment pattern virtually obscured by melanophores; the fins, the breast, belly, sides, and head are essentially black. The tip of the pelvic fin spine is swollen into a small white bulb. There are fleshy tips to the pectoral fin rays that are most conspicious on the more ventral fin rays. Males are larger than females (Raney and Lachner, 1943). Males of *E. perlongum* taken on March 26 (CU 30035, Lake Waccamaw) have much darker fins than the females, especially the first dorsal, anal, and pelvic fins. Fleshy tips are present on the distal ends of the pelvic fin elements, but these are not as prominent as in *E. nigrum* or in *E. olmstedi*. Cole (1957) did not find tubercles in any species of the *nigrum* group.

Six collections containing tuberculate males of *E. chlorosomum* have been examined. They were taken between March 8 (TNHC 2374, Texas, San Jacinto Co.) and April 17 (USNM 166172, Texas, Lake Belmont). The best developed male (UMMZ 161309, Louisiana, Lincoln Par., April 7, 39 mm.) has thin, elongated tubercles distributed along the entire length of the ventral surface of the first two pelvic rays, the proximal three-fourths of rays 3 and 4, and the proximal quarter of ray 5. Their presence on the proximal part of the pelvic fin is very unusual; most darters have them best developed distally. A few poorly developed tubercles are scattered on the middle portions of anal rays 2–5 of this specimen. The other tuberculate males show similar patterns, although the tuberculate areas are not as extensive. None of the females are tuberculate. The genital papilla of the female is a swollen rugose pad, differing from that in the *nigrum* group (low and flowerlike) and that in the *stigmaeum* group (an elongate tube). Males of *E. chlorosomum* are darker than females, especially the first dorsal, anal, and pelvic fins, and the venter, but there is no approach to the black fins present in males of the *nigrum* group. Winn (1958b, p. 188) reported Clark Hubbs's observation that *E. chlorosomum* spawns on plants or debris.

Thirteen collections of *E. jessiae* (UMMZ, VPI, CU, USNM) containing tuberculate males were examined. These collections were taken from March 13 (UMMZ 103591, Tennessee, Campbell Co.) to April 10 (UMMZ 103709, 103687, 103676, Tennessee, Anderson Co.). Most males have tubercles only on the ventral scale rows, but at maximum development in March (UMMZ 103567, 114852, 103591) poorly developed tubercles are present on the ventral surface of pelvic rays 3 and 4, and a few are also scattered on the anal fin rays. At maximum development, ventral scale tubercles begin shortly behind the pelvic fin origin on one row of scales and extend onto 4–7 rows per side just anterior to the genital papilla, 2–3 rows above each side of the anal fin base, and a total of 3–4 midventral caudal peduncle scale rows. Males have darker fins and venters than females and have enlarged lateral blotches. The genital papillae of breeding females are thin, elongate tubes totally unlike the genital papillae of breeding females of the *nigrum* group. There is little or no trace of the fleshy tips that develop on the pectoral and pelvic fin rays in the *nigrum* group. In life, breeding males (USNM 187735, Tennessee, Little Pigeon R., April 1) have 8–10 narrow blue bars on the body, the anal fin is blue with a white submarginal band, the dorsals are blue basally with a submarginal red band on the first dorsal and a submarginal white band on the second dorsal. The blue coloration also extends out onto the caudal fin.

The tubercle development of males of *E. stigmaeum* is quite similar to that described above for *E. jessiae*, except that the fin tubercles are better developed (especially in smaller specimens), and there is a puzzling type of geographic variation present. Males of *E. stigmaeum* from Kansas, Kentucky, and Tennessee (UMMZ, USNM) are very similar to males of *E. jessiae* in pigmentation, maximum size of males, and great development of ventral scale tubercles as contrasted with fin tubercles; however, most males from Alabama and Mississippi (UMMZ) are smaller, have less well-developed pigmentation, and have the fin tubercles well developed and the ventral scale tubercles almost absent. This is contrary to most tuberculate darters, which have tubercles better developed in more southern populations. Further study may show subspecific or specific differentiations.

Tubercles are present on males of the northern populations of *E. stigmaeum* from April 6 (UMMZ 165344, Kentucky, E. Fork Barren R.) to April 24 (USNM 163074–5, Kentucky, Green R.). At maximum development (UMMZ 171769, Kansas, Spring R., April 7), ventral scale tubercles start at a point one-third of the distance from the pelvic to the anal fin origin and extend onto three rows of scales per side just anterior to the genital papilla. Tubercles are not present on the scales above the anal fin base or on the ventral surface of the caudal peduncle in any of the males I have examined, but they will probably be found to be present when additional material is examined. One of the three 37 mm. males in this collection shows the best development of anal fin tubercles; they are present on the second anal spine and on all of the soft rays. Pelvic fin tubercles are developed distally to the fork on the ventral surface of pelvic ray 3 and on the entire length of rays 4 and 5. There seems to be a tendency for the fin tubercles to be best developed in smaller specimens and the ventral scale tubercles to be best developed in larger males.

In the southern population of *E. stigmaeum*, fin tubercles but not ventral scale tubercles are present on males from four collections taken from April 2 (UMMZ 155359, Mississippi, Bogue Chitto R.) to May 4 (UMMZ 166388, Alabama, Luxapallila Cr.). A 36 mm. male from UMMZ 155359 has tubercles on the distal three-fourths of all the anal soft rays but none on the spines. A 29 mm. male (UMMZ 163553, Alabama, Big Escambia Cr.) has a few small tubercles on the distal half of the second anal spine. The 36 mm. male has the best developed pelvic fin tubercles on the distal three-fourths of the ventral surface of pelvic soft rays 2–4. Males in one southern collection (USNM 166055, Alabama, Alabama Dr., April 6) have poorly developed pelvic fin tubercles, lack anal fin tubercles, and have ventral scale tubercles starting one-third of the way posteriorly from the pelvic to the anal fin origin and extending onto 3 rows of scales just anterior to

the genital papilla, 0–2 rows above each side of the anal fin base, and onto 3 ventral caudal peduncle scale rows. This collection matches the description of the northern populations of *E. stigmaeum* more closely than the southern ones.

In studying the breeding behavior of Kentucky and Tennessee populations of *E. stigmaeum*, Winn (1958b, p. 172) found that males are larger than females and have larger anal and pelvic fins. He reported the presence of tubercles on the anal and pelvic fins of males but failed to find any on the ventral body scales. Cross and Minckley (1958) described the coloration of breeding males and noted tubercles on the anal fin rays. In spawning, the male mounts the female in such a manner that his tuberculate pelvic fins are in contact with her dorsum and his tuberculate anal fin and ventral scales are in contact with her sides (Winn, 1958a; 1958b, fig. 4). This spawning position is similar to that found in a number of other darters such as *E.* (*Oligocephalus*) *caeruleum* and *E.* (*O.*) *spectabile* and is totally unlike the complex inverted spawning position of the *nigrum* species group of *Boleosoma*. Winn (1958b, p. 188) felt that the placement of *stigmaeum* in *Boleosoma* should be reconsidered.

Subgenus *Ioa* Jordan and Evermann

The only known species is *E. vitreum* (Cope). Specimens taken from March 28 to May 17 (CU, UMMZ) lack tubercles. The males are larger than the females and become much darker in the breeding season, especially on the cheeks and venter. The genital papilla of the breeding female has many free fleshy villi. Winn and Picciolo (1960) noted the pigment differences between the sexes and did not mention the presence of breeding tubercles. They reported that *E. vitreum* spawns communally in mid-April on a solid surface in the path of a strong current. This behavior may have evolved from spawning under rocks practiced by some members of the subgenus *Boleosoma*. Winn and Picciolo listed several similarities between *E. vitreum* and *E. nigrum* in support of this hypothesis: the sexes are beside each other during spawning; one egg is laid at a time on a hard surface; males are very black in the breeding season; and females of both species have a complicated flowerlike genital papilla. The lack of breeding tubercles in *Ioa* and the *E.* (*Boleosoma*) *nigrum* species group further confirms this relationship.

Subgenus *Etheostoma* Rafinesque

Fifteen species are presently placed in this subgenus. The subgenus can be divided into two different tuberculate species groups and one nontuberculate group. Members of the *variatum* group, *variatum*

Kirtland, *tetrazonum* (Hubbs and Black), *euzonum* (Hubbs and Black), *kanawhae* (Raney), and *osburni* (Hubbs and Trautman) have breeding tubercles on the ventral scales in both sexes. This appears to be the only group of darters with both sexes tuberculate. (In the Romanichthyini, both sexes of *Zingel* and *Romanichthys* are tuberculate.) Species of the *variatum* group are heavy-bodied darters with prominent dorsal saddles. Breeding males of many of the species have bright colors. Species of the *inscriptum* group, *inscriptum* (Jordan and Brayton), *thalassinum* (Jordan and Brayton), *swannanoa* Jordan and Evermann, *blennioides* Rafinesque, and *gutselli* (Hildebrand), have similar but less prominent tubercles present only on the males. The tubercles in both groups, unlike the more conical ones present in most other percids, are low whitened pads on the free posterior edges of the ventral and lateral scales. The nontuberculate *zonale* group includes *zonale* (Cope), *rupestre* Gilbert and Swain, *histrio* Jordan and Gilbert, and probably *blennius* Gilbert and Swain. *E. sellare* (Radcliffe and Welsh) is apparently also nontuberculate, but it does not seem to be related closely to any of the three species groups.

Breeding tubercles are present on *E. variatum* from as early as October 5 (USNM 161783, Pennsylvania, Allegheny R.) until May 12 (CU 43070, New York, Allegheny R.). No tubercles are present on Allegheny River specimens taken in June or August. The October 5 collection has 27 females and 18 males (57–70 mm. in standard length) without tubercles and 8 males (60–66 mm.) with small tubercles on 2 rows of midventral scales per side just anterior to the genital papilla and on 4 rows on the midventral portion of the caudal peduncle. Four females (58–67 mm.) taken October 13 (USNM 161786) also lack tubercles while a 74 mm. male has small tubercles on 4 ventral scale rows per side just anterior to the genital papilla and on 4 midventral rows on the caudal peduncle. By April 19 (CU 34938) tubercles are present on 5 rows of ventral scales per side just anterior to the genital papilla. Females taken April 20 (CU 8226, fig. 5) have tubercles on about 6 rows of belly scales per side just anterior to the genital papilla. William J. Richards kindly called my attention to a male taken April 29 (CU 41893, New York, Allegheny R.) that has tubercles on the approximately 20 breast scales, on all the belly scales up to 6 rows per side just anterior to the genital papilla, 4–5 rows above the anal fin base, and 7 midventral scale rows on the caudal peduncle. Both May 12 males (CU 43070, 69–70 mm.) have tubercles extending onto 7 rows per side just anterior to the genital papilla. These males and CU 41893 also have tubercles on the ventralmost 2 rows of scales which extend onto the lower part of the caudal fin. The presence of breeding tubercles in *E. variatum* has not previously been reported although tubercles are plainly visible in a photograph of a breeding male (Hubbs

and Black, 1940, pl. 2, fig. 1). The tips of the pelvic elements are more swollen in males in CU 8226 than in females. The genital papillae of females are elongate tubes. The pelvic and anal fins of females are only slightly pigmented while those of breeding males are completely black, except for white fleshy tips on the anterior elements in both fins. The pectoral fins of females are banded, while in breeding males they are completely black. The breast and belly of females are nearly immaculate, while those of males are completely covered with melanophores. Both dorsal fins of males are more heavily pigmented than those of females. Lachner, Westlake, and Handwerk (1950) reported that males of *E. variatum* were larger, brighter, and more highly pigmented, and that they had larger pelvic and dorsal fins than females.

FIGURE 5.—Male of *Etheostoma* (*Etheostoma*) *variatum* showing the distribution of breeding tubercles (CU 8226, Pennsylvania, Shenango River, April 20, 72 mm. SL).

Males of *E. tetrazonum* taken in Missouri March 16 to April 6 (CU 32879, 37380, 37354; KU 7537) have tubercles on all the breast scales, on 3–5 rows of scales per side just anterior to the genital papilla; 1 row above the anal fin; and a total of 7 ventral caudal peduncle rows. The tubercles are best developed on the largest males but are obvious on other males down to 47 mm. standard length. Females have lower and much less prominent tubercles on 6 rows of midventral scales. Males are much darker than females, with the second dorsal, pelvic, and anal fins almost black. Bands on the pectoral, second dorsal, and caudal fins of females are completely obscured by dark pigment in males. The head, breast, and belly of males are also much darker than in females.

Tubercles are present on *E. euzonum* taken April 4 (CU 32900, Missouri, White R.), April 7 (KU 7634, Missouri, Current R.), and April 30 (TU 10175, Arkansas, White R.). In males they are present on the breast scales, on about 7 scale rows per side just anterior to the

genital papilla, 3 rows above the anal fin base, and 6–7 rows of ventral scales on the caudal peduncle. Females have a similar tubercle distribution, but the tubercles are smaller and do not extend as far dorsally. Tubercles are absent in specimens (UMMZ) taken in July and August.

The same tubercle distribution is present on specimens of *E. kanawhae* taken from April 1 (UMMZ 131838, North Carolina, New R.) to June 8 (USNM 162196 and 162197, Virginia, New R.). Males with maximum tubercle development (USNM 162197) have tubercles on 2 rows of scales at the pelvic fins extending onto 7 rows of scales per side just anterior to the genital papilla, 4 rows above each side of the anal fin base, and a total of 8 rows on the ventral caudal peduncle scales. The maximum development of tubercles observed in females is on a 66 mm. specimen from the same collection. Here tubercles also begin at the pelvic fins and extend onto 7 rows of scales just anterior to the genital papilla, but are present on only 2 rows of scales above each side of the anal fin base and on only 5 rows of caudal peduncle scales. Small tubercles are present on three males taken July 23 (UMMZ 165448, North Carolina, Little R., 57–66 mm.), but they are absent from a 61 mm. female from the same collection. Faint traces of tubercles are barely discernible on males taken as late as August 24 (UMMZ 169360, Virginia, Little Reed Island Cr.). In the original description of *E. kanawhae*, Raney (1941) mentioned that the holotype, as well as other males taken near the breeding season, had the scales on the belly and lower sides "tipped with pearl white." Tubercles are clearly visible in his photograph of a male paratype.

Tubercles are present on specimens of *E. osburni* taken between May 17 (USNM 117588, paratype; and UMMZ 95370, Virginia, Reed Cr.) and July 15 (UMMZ 118800, West Virginia, Indian Cr.); they are absent from specimens taken in August and October. At maximum development males have tubercles on 5–7 rows of midventral scales per side just anterior to the genital papilla, 3–5 rows above each side of the anal fin base, and on 4–8 rows on the caudal peduncle. Some of these tubercles have points on their posterior ends. Females have a similar distribution of tubercles, but they are lower, broader, and lack the points present on males. Males are darker than females, especially the pelvic, anal, and second dorsal fins, and the head. In their original description of *E. osburni*, Hubbs and Trautman (1932) did not mention the presence of breeding tubercles, but they can be seen in their figure of the holotype (UMMZ 92409). They are also present on a paratype (USNM 117588).

Thus the intimate relationships of the five species in the *variatum* group as noted by Hubbs and Black (1940) and Raney (1941) are

further corroborated by similarities in the distribution of breeding tubercles. With reservations, Hubbs and Black included *E. blennius* in their *variatum* group; I would tentatively remove it since it appears to be nontuberculate. They considered the possibility that *E. sellare* might belong to the *variatum* group; I feel this is highly unlikely.

Tubercle distribution in the *inscriptum* group is similar to that in the *variatum* group, but the tubercles are not on as many areas nor are they present in females. Tubercles are present on males of *E. inscriptum* in the Savannah Drainage at least from March 25 (CU 19548, 19755) until June 3 (CU 37935). At maximum development (USNM 165732, Georgia, Altamaha Dr., April 5), tubercles start one-fourth of the way posteriorly from the pelvic fin origin to the anal origin and extend onto 4 rows of scales per side just anterior to the genital papilla, 3 rows above the anal fin base and 5 ventral caudal peduncle rows. Males are much darker than females, especially the dorsal, anal, and pelvic fins, and the breast and the belly. There are two concentrations of pigment on the membranes of the first dorsal fin of males, anteriorly between the first 3 spines and posteriorly between the last 2 spines. The tips of the pelvic spine and, to a lesser extent, the lower pelvic rays are swollen in males. The general banded pattern of females is obscured by the increased body pigmentation of breeding males. The genital papilla of the breeding female is a very long thin tube.

E. thalassinum from the Santee Drainage of North and South Carolina has virtually the same tubercle pattern as *E. inscriptum*. Tubercles are present at least during the period March 23 (USNM 187567, 187580; CU 10113, 19662; UMMZ 138494) until April 20 (USNM 187578, 187582). Four females collected on February 27 (USNM 187576) are filled with large eggs and I believe males are probably tuberculate at this time. The maximum development of tubercles observed is on a 57 mm. male taken on April 19 (USNM 187573). Tubercles start posteriorly one-fourth of the way from the pelvic fin origin to the anal origin and extend onto 4 rows of scales per side just anterior to the genital papilla, 3 rows above the anal fin base, and a total of 5 ventral caudal peduncle rows. Tubercles are less well developed in the earlier part of April. Tubercles are absent from males taken June 25 to November 6. All females lack tubercles. Males are darker than females, especially the pelvic and anal fins, which in females are immaculate.

Males of *E. swannanoa* taken between April 1 (UMMZ 138521, Virginia, Holston R.) and June 7 (CU 37886, North Carolina, French Broad R.) have tubercles on the ventral scales. At maximum development (UMMZ 138482, North Carolina, Swannanoa R.), the tubercles begin one-third of the way posteriorly from the pelvic fins to

the origin of the anal fin and extend onto 4–5 rows of scales per side just anterior to the genital papilla, 3–4 rows above each side of the anal fin base, and 5 rows of ventral scales on the caudal peduncle. Specimens collected from June 17 to August 15 (UMMZ) lack tubercles. Females also lack tubercles. Females of *E. swannanoa* have the longest genital papillae in relation to body size that I have found in any darters. A 61.4 mm. female had a genital papilla 5.9 mm. long.

I have examined four collections containing tuberculate males of *E. blennioides*. In addition, Dr. Robert V. Miller, who is presently reviewing the taxonomy of this species, has kindly provided me with his notes on tubercles and called my attention to two collections containing tuberculate specimens. Tubercles are present on males of *E. blennioides* at least as early as March 24 (CU 37520, Kentucky, Licking R.) until June 26 (UMMZ 96357, Tennessee, Cumberland R.). At maximum tubercle development (CU 20629, Pennsylvania, Genesee R., April 27), tubercles start a third to halfway posteriorly from the pelvic fin origin to the anal fin, extend onto 4–6 rows per side just anterior to the genital papilla, 1–3 rows above each side of the anal fin base, about 5–6 rows of ventral caudal peduncle scales, and are found also on some of the small scales at the ventral part of the base of the caudal fin. By June 26 (UMMZ 96357), tubercles have almost disappeared. Spawning occurs in New York between April 13 and June 12 (Fahy, 1954, p. 167), so there is a good correlation with the presence of tubercles. Tubercles are absent on females. Winn (1958b, p. 172) and Lachner, Westlake, and Handwerk (1950) reported that males were larger than females and had larger first dorsal and anal fins. Winn also reported that males had larger pectoral and pelvic fins. Lachner et al. found the pelvic fins of both sexes to be of about equal size, the second dorsal fin larger and the pectoral fin smaller in males. The tips of the pelvic spines and most of the soft rays are slightly more swollen in breeding males than in breeding females. Males are much darker, especially the head, venter, and body, and the pelvic and anal fins.

E. blennioides spawns at a horizontal to a vertical angle, usually at about 45° (Winn, 1958a; 1958b). Spawning takes place over *Cladophora*-covered rocks in the deepest and swiftest parts of stream riffles (Fahy, 1954, p. 169). The male mounts the females with his pelvic fins over her dorsum and his tuberculate lower sides in contact with her sides (Winn, 1958a; 1958b, fig. 4).

In his studies on *E. gutselli*, Miller has found only two tuberculate specimens, which he has generously permitted me to examine. Both are males, 87 and 91 mm. long, taken in the northeastern corner of Georgia May 9 (UG uncat.). Small, low tubercles begin halfway posteriorly from the pelvic fins to the anal fin origin and extend onto

4 rows of scales per side just anterior to the genital papilla. A few tubercles are present on the scales above the origin of the anal fin base, but they are absent posteriorly. Miller has not found tubercles on any females of this species. Males are very dark with the lateral markings almost obscured. The tubercle and pigment patterns of *E. gutselli* confirm its close relationship to *E. blennioides*.

Four of the five remaining species currently placed in the subgenus *Etheostoma* can be assigned to the nontuberculate *zonale* group. These are *rupestre*, *zonale*, *histrio*, and probably *blennius*. Proper allocation of the fifth species, *E. sellare*, is difficult at present. Hubbs and Black (1940) considered that it might belong to the *variatum* group because of its bold back markings. However, the two types of *E. sellare* are both spring-caught females and lack tubercles, rendering this unlikely. I do not feel that it is closely related to any of the three species groups of the subgenus *Etheostoma*, but I cannot suggest a better group to place it in.

Specimens of *E. rupestre* taken in April and May (USNM 166029 and UMMZ 166372, Alabama, Tombigbee R.; TU 19896 and UMMZ 171762, Alabama, Cahaba R.) lack tubercles. Both males and females have the tips of the pelvic spines and most of the soft rays tipped with cream-colored fleshy knobs. Females have the anal and pelvic fins and the breast and belly immaculate, whereas males have these areas and the dorsal fins very dark. The testes and ovaries of these specimens are greatly enlarged. Specimens of *E. zonale* in 16 collections (USNM, UMMZ) taken from March 1 (TU 8170, Mississippi, Pearl R.) to June 21 (UM 5219A) lack tubercles. The pigmentation differences between the sexes are very similar to those in *E. rupestre*. Lachner, Westlake, and Handwerk (1950) reported that males of *E. zonale* were larger than females and had larger dorsal fins. Specimens of *E. histrio* in August, October, and January collections (USNM, UMMZ) and in a March 25 Texas collection (TNHC 1114) are nontuberculate. Males of *E. histrio* taken in January and March have greatly enlarged testes and the females are filled with large eggs. Spring caught specimens of *E. blennius* (UMMZ) lack tubercles, but sufficient material has not yet been examined to be sure this species belongs to the *zonale* group.

Subgenus *Ulocentra* Jordan

There are four described species: *atripinne* (Jordan), *coosae* (Fowler), *duryi* Henshall, and *simoterum* (Cope), plus about nine undescribed species, in this subgenus (R. M. Bailey, pers. comm.). I have examined some breeding material of all described species as well as a number of the manuscript forms (mostly UMMZ specimens). Males of all species are brightly colored in life and apparently lack breeding

tubercles. In the absence of tubercles, as well as in other characters, the subgenus *Ulocentra* seems most closely related to the *Etheostoma* (*Etheostoma*) *zonale* species group.

Winn (1958b, p. 172) noted that males of two of the undescribed forms of *Ulocentra* (from the Barren and Green rivers of Kentucky) were larger than the females, had larger anal, first dorsal, and pelvic fins, and lacked breeding tubercles. These two species usually spawn in a nearly vertical position with the male mounted on the female's back (Winn, 1958a; 1958b, fig. 4).

Subgenus *Allohistium* Bailey

There is only a single species: *E. cinereum* Storer. The testes and pigmentation of a spring-caught male (CU 37281, Tennessee, Cumberland R., March 26, 56 mm.) are well developed and breeding tubercles are absent. Males in six collections taken later in the year (ANSP, UMMZ, USNM) have slightly developed testes and also lack tubercles.

Subgenus *Nothonotus* Agassiz

There are seven described species in this subgenus: *acuticeps* Bailey, *camurum* (Cope), *jordani* Gilbert, *maculatum* Kirtland, *moorei* Raney and Suttkus, *rufilineatum* (Cope), and *tippecanoe* Jordan and Evermann. Apparently this subgenus lacks breeding tubercles, although I have not examined adequate breeding material of *acuticeps* or *tippecanoe*.

Bailey (1959) described the sexual dimorphism in color as well marked in *Nothonotus*. He wrote (p. 3): "All species are colorful, varying from subdued to gaudy. The breast is blue or green in adult males . . . . The body is lined with dark in several species; the soft dorsal, caudal, and anal fins are dark-edged in some, and the fins may be somber or brightly colored with red, orange, or green . . . . No species has a submarginal red or orange band in this [first dorsal] fin." For *E. acuticeps*, he reported (p. 8): "It is probable that no nuptial tubercles are developed since adults taken in June, and nearly ready to spawn, have none." Raney and Suttkus (1964) reported that nuptial tubercles are absent in *E. moorei*. Raney and Lachner (1939) noted that males of *E. maculatum* attain a larger size than females. In addition, Winn (1958b, p. 172) reported that males have larger anal, first and second dorsal, pectoral, and pelvic fins than females. He described the genital papilla of the breeding female as flattened and flowerlike, and he did not find breeding tubercles on the male. *E. maculatum* spawns under rocks and the male defends the nest (Raney and Lachner, 1939). *E. camurum* spawns in gravel around or under

rocks in a spawning position similar to that described by Winn (1958b, fig. 4) for *E. caeruleum* (Mount, 1959).

Subgenus *Oligocephalus* Girard

Twenty-one species are presently placed in this, the largest subgenus of *Etheostoma*. There appear to be three different tuberculate species groups and one nontuberculate group. Males of the *nianguae* group, *nianguae* Gilbert and Meek and *sagitta* (Jordan and Swain), have conical tubercles on the ventral scales. Males of the *radiosum* group, *radiosum* (Hubbs and Black), *whipplii* (Girard), and *caeruleum* (Storer) have tubercles that are similar to but not as high as those in the *E. nianguae* group. Eight other tuberculate species may best be placed together for the present, although they differ from one another in the details of tubercle distribution: *punctulatum* (Agassiz), *fricksium* Hildebrand, *hopkinsi* (Fowler), *parvipinne* Gilbert and Swain, *spectabile* (Agassiz), *luteovinctum* Gilbert and Swain, *pallididorsum* Distler and Metcalf, and *cragini* Gilbert. The species in the *spectabile* group

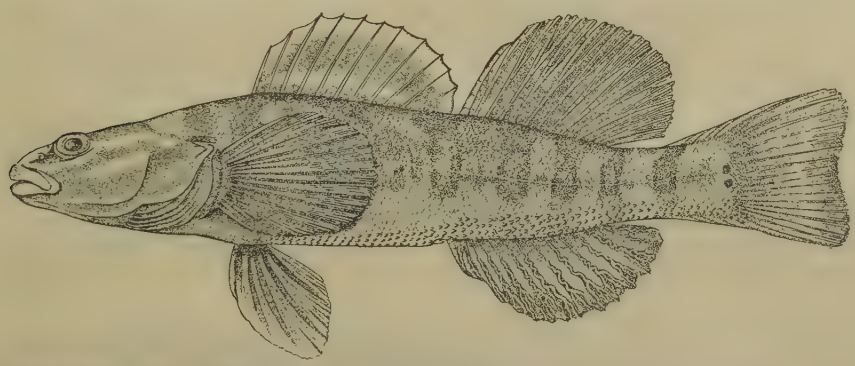

FIGURE 6.—Male of *Etheostoma* (*Oligocephalus*) *nianguae* showing the distribution of breeding tubercles (CU 32888, Missouri, Osage River, March 16, 89 mm. SL).

differ from the two previous groups in having tubercles on the anal fin. Two of the species in this group have tubercles on only the anal fin, while the others also have them in additional regions. This leaves a residue of eight species which appear to be nontuberculate: *asprigene* (Forbes), *swaini* (Jordan), *mariae* (Fowler), *juliae* Meek, *pottsii* (Girard), *lepidum* (Baird and Girard), *exile* (Girard), and *grahami* (Girard).

A fine breeding male of *E. nianguae* (CU 32888, Missouri, Miller Co., Big Tavern Cr., Mar. 16, 1957, a specimen overlooked by Kuehne and Bailey, 1961) has breeding tubercles well developed on about 12 mid-ventral scale rows just anterior to the genital papilla (fig. 6). There are no tubercles on either the pelvic or anal fins. There is, however, a

sinuous ridge of fleshy material extending along each element of the anal fin. A 51 mm. male of *E. sagitta sagitta* (USNM 144485, Kentucky, Cumberland R., April 8) has tubercles on the ventral scales beginning halfway posteriorly from the pelvic to the anal fin and extending onto 3–4 rows of scales per side just anterior to the genital papilla. The tubercles are high and conical. None are present above the anal base or on the lower surface of the caudal peduncle. However, a larger specimen from the same field collection (UMMZ 144492) has tubercles on 2 rows of scales above each side of the anal fin base and on 5–6 midventral rows on the caudal peduncle, as Bailey (1948) has previously noted. I have not yet examined a tuberculate specimen of *E. sagitta spilotum* Gilbert. The similarity of breeding tubercle distributions further confirms the intimate relationships of *E. nianguae* and *E. sagitta* as pointed out by Bailey (1948, in describing the subgenus *Litocara* for the three forms), and Kuehne and Bailey (1961).

There are tubercles on the ventral scales of males of *E. radiosum* in nine collections taken between April 4 and April 25 in the Red River drainage of Oklahoma and Arkansas: USNM 165772, 165797, 165865, 165866; UMMZ 161368 holotype, UMMZ 161369, and MCZ 37205 paratypes of *E. radiosum paludosum* (Moore and Rigney); USNM 153532 and MCZ 37204, paratypes of *E. radiosum cyanorum* (Moore and Rigney). A 52 mm. male from USNM 153532 has the best developed tubercles, located on 3 rows of ventral scales starting about one-fourth of the way from the pelvic origin to the anal origin. They are slightly raised, circular mounds on the posterior edge of the scales, not pads as in the *variatum* group. The tubercles on the ventralmost scales have elongate points on their posterior end. Just anterior to the genital papilla, tubercles are present on about 6 scale rows per side. They are on 5 rows of scales above each side of the anal fin base and on 7 midventral rows of scales on the caudal peduncle. The tubercle patterns are similar in the larger males in the other collections, but the tubercles are smaller and are not developed on as many scale rows. None of the more than 120 females in these collections show any sign of tubercle development and all the larger females have the ovaries filled with large eggs. The genital papilla of the female is an elongate cone. The pelvic fin and venter of the female are immaculate, the anal fin is moderately pigmented, and the dorsal fins are somewhat blotched and banded. In the male, the pelvic fin and venter are very dark, the dorsals, anal, and caudal fin are heavily pigmented on the basal half and have a light (orange in life) strip followed by a dark distal edge to the fin. In their original description of *E. radiosum paludosum*, Moore and Rigney (1952) reported tubercles on the bellies of males. In spawning, the female *E. radiosum cyanorum* partially buries herself in sand

and the male mounts her with his pelvic fins clasped over her dorsum and his tail pressed tightly against hers (Linder, 1958).

The same tubercle pattern was found on males of *E. whipplii* taken between February 29 (UMMZ 177250, Arkansas, Illinois Bayou) and April 12 (TU 17771, Texas, Neches R.). At the maximum development observed (UMMZ 155103, Kansas, Crooked Cr., April 9; and UMMZ 177160, Arkansas, Illinois Bayou, April 3), tubercles begin one-third of the way from the pelvic fin origin to the anal fin origin, extend onto 5–7 rows of scales per side just anterior to the genital papilla, on 2–3 rows above each side of the anal fin base, and onto 6–8 midventral rows of caudal peduncle scales. Specimens taken earlier (UMMZ 177250, February 29) and later (TU 17771, April 12) lack tubercles above the anal fin base and on the ventral surface of the caudal peduncle.

The tubercle pattern of *E. caeruleum* seems to be the same as that of *E. radiosum* and *E. whipplii*. Leslie W. Knapp, who is reviewing the systematics of *E. caeruleum*, has kindly given me his data on tubercles of this species and has permitted me to examine the specimens with the best developed tubercles. Poorly developed tubercles are present in 15 collections taken in Missouri and Arkansas between March 27 (CU 37190, Missouri, Madison Co.) and June 5 (KU 5605, Missouri, Gasconade R.). Males from an Illinois collection (INHS uncat., Rock R., April 25) are at the height of breeding color according to Knapp and show the best development of tubercles. A 51 mm. male from this collection has tubercles present on the belly scales starting halfway from the pelvic to the anal fin origin and extending onto 4 rows of scales per side just anterior to the genital papilla, on 2–3 rows above the anal base, and on about 5 midventral rows on the caudal peduncle. There are no tubercles on the fins of these or many other breeding males examined. Winn (1958b, p. 172) reported that males of *E. caeruleum* are larger than females and have larger anal, first dorsal, pectoral, and pelvic fins, but he failed to find breeding tubercles. In spawning, the female of *E. caeruleum* partially buries herself in the gravel of the stream bottom and the male mounts her (Winn, 1958a; 1958b, fig. 4). Since the belly and sides of the male are then in contact with the sides of the female, the tubercles may assist him in maintaining his position.

Temporarily, at least, the other eight tuberculate species of the subgenus *Oligocephalus* may be placed together in the *spectabile* group based on the presence of breeding tubercles on the anal fin of males. *Etheostoma parvipinne* and *E. fricksium* have tubercles on the anal fin alone. The other six species, *hopkinsi*, *cragini*, *punctulatum*, *luteovinctum*, *pallididorsum*, and *spectabile*, have tubercles in other areas as well. Females of all six species lack tubercles.

Numerous males of *E. parvipinne* taken early in 1952 in a tributary of the Yazoo River, Mississippi, have tubercles on the anal rays. A 55 mm. male taken February 22 (USNM 196636), has tubercles on the distal fourth of the first anal soft ray, the distal half of the second ray, the distal half to two-thirds of rays 3–5, and the distal third of rays 6–7. There are no tubercles on the anal spine or the last anal soft ray. Males taken later in the spring (exact dates unknown) have similar tubercle distributions, but the tubercles are larger and extend farther proximally on the rays. (Some specimens from the original collections, UM 47 and 521A, have been recatalogued as USNM 196636, 196637, UMMZ 162907.) Two 44 mm. males taken March 7 (TNHC 2835, Texas, Montgomery Co.) have tubercles developed on the distal half to three-fourths of all anal soft rays. There are no pelvic or body tubercles on any of the specimens. The belly and pelvic fins of the females are immaculate. These areas, plus the anal and dorsal fins, are dark in the males. Males taken from April 4 to April 22 (UMMZ) lack tubercles.

Bailey and Richards (1963) stated that breeding tubercles are present on the lower surface of the pelvic fin, anal fin, and on the ventral body scales of breeding males of *E. hopkinsi*. Richards has very kindly called my attention to the only tuberculate specimens he has examined. Males of *E. hopkinsi binotatum* Bailey and Richards are tuberculate from as early as March 25 (CU 19604, S.C.) until April 29 (UG 283, Georgia) in the Savannah River drainage. The maximum development of tubercles is on a 39 mm. male collected March 27 (CU 19600, South Carolina, Savannah Dr.). A few tubercles are present on the distal tip of the second anal spine and 5–10 prominent tubercles are present on all the anal soft rays except the last half of the last ray. Small but prominent tubercles are developed on the ventral surface of the proximal portion of pelvic soft rays 3–5. Tubercles (and scales) begin halfway posteriorly from the pelvic fins to the origin of the anal fin and extend onto 3–4 rows of scales per side just anterior to the genital papilla. No tubercles are present above the anal fin base or on the ventral surface of the caudal peduncle.

Dr. Richards has also permitted me to examine the tuberculate specimens he has found of *E. fricksium*. A few very small tubercles are on anal soft rays 3–6 of two males (CU 17375, Georgia, Savannah Dr., 46–50 mm.) taken March 24. Tubercles are also present on the anal rays of males taken in the Edisto drainage (CU 29850, South Carolina, March 28). Additional tuberculate specimens are needed to determine whether tubercles develop on the pelvic fins and venter of *E. fricksium* as they do on *E. hopkinsi*. If not, tubercle pattern will be one additional difference between the two species which had been confused until recently (Bailey and Richards, 1963).

Tubercles were found on males of *E. cragini* collected from January 1 (UMMZ 156694, Kansas, Meade Co.) to May 7 (KU 5658, Missouri, Shoal Cr.). Tubercles are best developed on two males from UMMZ 156694 (30 and 31 mm.), on the 50 mm. male syntype of the nominal species *E. pagei* Meek (USNM 45566, Missouri, Neosho R., Apr. 15, 1893), and on a specimen collected April 5 (CU 32919, Missouri, Neosho R., 32 mm.). In the latter specimen, tubercles are present on most of the length of the anal spines and soft rays, on the distal two-thirds of the pelvic spine, and the distal third of the first three pelvic soft rays (ventral surface). No tubercles are present on the dorsal surface of the pelvic rays in this specimen, but there are a few tubercles on the distal tip of pelvic rays 1 and 2 in KU 7233. On the CU specimen, tubercles also are present on the ventral scales starting posteriorly one-third of the distance from the pelvic to the anal fin origin. They extend onto about 5 rows of scales per side just anterior to the genital papilla and onto 2–3 rows above each side of the anal fin base. No tubercles are present elsewhere on these specimens nor are they present on the females. Tubercles are absent from the abundant UMMZ material of *E. cragini* collected in June, July, and August. Moore and Cross (1950) reported tubercles on the anal rays of males of *E. cragini* taken January 1 (UMMZ 156694). They also found tubercles on the pelvic fins, the ventral scale rows near the anal base, and along the belly of breeding males taken February 2 in Mayes Co., Oklahoma.

A similar tubercle distribution is present on some of the paratypes of the closely related *Etheostoma pallididorsum*. Nine males collected April 6 (KU 6158, Arkansas, Caddo R.) are tuberculate. All have tubercles along both anal spines and on all the anal soft rays. Pelvic fin tubercles are poorly developed on the 5 smaller specimens (29, 31, 33, 34, and 35 mm.), better developed on two larger specimens (35 mm.), and best developed on the two largest specimens (37 mm.). Here they are present on the distal three-fourths of the pelvic spine and first pelvic soft ray (dorsal and ventral surfaces), the distal three-fourths of ray 2 (ventral surface), and distal half of ray 2 (dorsal surface), the distal third of ray 3, and the distal quarter of ray 4 (ventral surface only). The ventral scale tubercles are best developed on a 35 mm. male where they begin halfway between the pelvic and the anal fins, extend onto 4 rows of scales per side just anterior to the genital papilla, 2 rows above each side of the anal fin base, and are present on the ventral surface of the caudal peduncle. Tubercles are absent in another collection of paratypes (USNM 196547) taken June 28. The identical tubercle distributions in *E. pallididorsum* and *E. cragini* serve as further evidence of their very close relationship. In their original description, Distler and Metcalf (1962) reported

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tubercles on the anal fin rays and on the belly scales of the paratypes described above.

Males of *E. punctulatum* in seven collections (UMMZ, KU, CU, TU) taken from January 30 (TU 22993, Oklahoma, Neosho R.) to May 2 (TU 2251, Oklahoma, Arkansas R.) have tubercles. They are present on the anal spines and soft rays of males taken in this period but are best developed on the soft rays. A 54 mm. male (CU 37346, Missouri, Osage R.) taken March 28 has the maximum tubercle development observed. There are 15–20 tubercles on each anal soft ray, fewer on the anal spines. Tubercles are present on the ventral surfaces of all pelvic fin elements, ranging in number from 5 (on the spine) to 30 (on the second soft ray). Tubercles are present on the dorsal surfaces of pelvic soft rays 1–3 as well as on the ventral surfaces. Tubercles are also present on about 7 rows of the ventral scales per side just anterior to the genital papilla and on about 6 rows along each side of the anal fin base. There are a few small tubercles on the ventralmost principal caudal ray.

Males of *E. luteovinctum* are tuberculate from at least March 26 (CU 37235) until April 28 (UMMZ 121612) in Duck River, Tennessee. Tubercles develop earliest and remain for the longest period of time on the anal fin. Except for tubercles on the anal spines, the males in CU 37235 have the best developed tubercles of the specimens examined. No tubercles are present on the first anal spine, a few are present on the second anal spine, and there are 5–10 tubercles on each of the anal soft rays. There are no tubercles on the ventral surfaces of the pelvic fin elements, but four intermediate-sized specimens have several tubercles distally on the dorsal surface on soft rays 1 and 2. Ventral tubercles start halfway from the pelvic to the anal fin and extend onto 4–5 scale rows per side just anterior to the genital papilla, 3 rows along each side of the anal base, and 5 midventral rows on the caudal peduncle. A few tubercles are present on the ventralmost principal caudal ray in the largest specimen. No tubercles are present on the pectoral fin. Some males (UMMZ 120985) have tubercles on the first instead of the second anal spine. Others (UMMZ 121259) have tubercles on both anal spines, although the tubercles are not as well developed in the other regions as in CU 37235. The nine collections with tuberculate males contained no tuberculate females.

Tubercles are present on the anal, pelvic, pectoral, and caudal fins and on the ventral scales of the males of *E. spectabile*. I have found tubercles on males of *E. s. spectabile* taken in late March (CU 37240, Missouri, Osage R.; CU 37496, Tennessee, Barren R.; CU 37436, Arkansas, White R.) and in early April (CU 38406, Missouri, Osage R.). Tubercles are present on 61 males (26–42 mm. standard length)

of *E. spectabile pulchellum* (Girard) taken April 20 (USNM 165807, Oklahoma, Poteau R.). At their maximum development, tubercles are present along the entire length of the anal fin elements and on the ventral surfaces of all the pelvic soft rays. Tubercles are also developed on the dorsal surfaces of pelvic soft rays 1–3 and on the anterior surfaces of pectoral rays 6–8. There are tubercles on about 4 rows of ventral scales per side just anterior to the genital papilla, on 4–5 rows above the anal fin base, and on 8 midventral rows on the caudal peduncle. A few males (CU 37436, fig. 7) have scattered small tubercles on the lower caudal rays. Males of *E. spectabile* are much

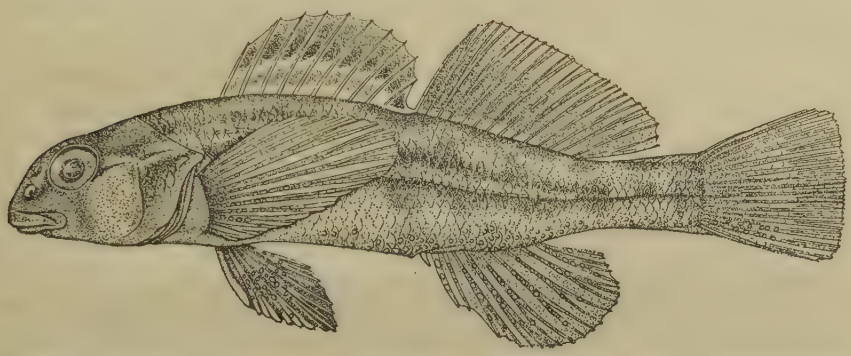

FIGURE 7.—Male of *Etheostoma* (*Oligocephalus*) *spectabile* showing the distribution of breeding tubercles (CU 37346, Arkansas, White River, March 29, 44 mm. SL).

darker than females, especially the pelvic, anal, dorsal, pectoral, and caudal fins, and on the breast and belly. The tips of the pelvic fin spine and, to a lesser extent, the pelvic and lower pectoral fin rays, have slightly swollen, unpigmented tips. Winn (1958b, p. 172) reported that males of *E. s. spectabile* were larger than females and had larger anal, first dorsal, pectoral, and pelvic fins, but he found no tubercles. In spawning, the male mounts the female after she has buried herself in the gravel of the bottom of the stream bed (Winn, 1958a; 1958b, fig. 4; Linder, 1958). The tuberculate pelvic fins of the male are in contact with the female's back; and his belly, sides, and caudal peduncle are pressed against hers.

The residual, apparently nontuberculate group of eight species of *Oligocephalus* (*asprigene, exile, grahami, juliae, lepidum, mariae, pottsii* and *swaini*) probably are not closely related to each other. Certainly they are quite diverse in general body form and pigmentation. The following list of numbers and sources of collections with included dates shows the relative adequacy of coverage of the species in this group: *asprigene*, 6 collections, Nov. 21 to June 16 (CU, USNM, TU, UMMZ); *exile*, 6 collections, May 14 to August 26 (UMMZ); *grahami*

(UMMZ 162135, Mexico, Nuevo Leon, Dec. 19, 14 males, 27–36 mm., and 35 females; TNHC 1971, Texas, Val Verde Co., April 14, 10 males, 29–40, mm., and 14 females; testes of males in both collections greatly enlarged and females filled with large eggs); *juliae*, 11 collections, Oct. 25 to Aug. 22 (TU, CU, UMMZ); *lepidum*, 6 collections, Feb. 4 to June 25 (CU, UMMZ, USNM); *mariae*, 5 collections, April 1 to June 29 (CU, UMMZ, TU, USNM); *pottsii* (USNM 162482, Feb. 14; USNM 55855, no date; TNHC 4032, June 26; testes enlarged in males, females filled with large eggs); and *swaini*, 5 collections, Jan. 28 to April 4 (TU, CU, UMMZ). Winn (1958b) found that females of *E. exile* are larger than males. Males have larger anal and first dorsal fins and lack breeding tubercles. Spawning takes place at a slight angle over organic debris and fibrous mud banks with the male mounted on the female's back (Winn, 1958a; 1958b; fig. 4). Strawn (1955a, 1955b) described the breeding colors of *E. lepidum* and *E. grahami* but did not mention breeding tubercles.

Subgenus *Villora* Hubbs and Cannon

There are two species in this subgenus: *E. okaloosae* (Fowler) and *E. edwini* (Hubbs and Cannon). I have examined virtually all the available material of *edwini* and Ralph W. Yerger has done the same for *E. okaloosae* (see Collette and Yerger, 1962). Both sexes of both species are nontuberculate. Males of *E. edwini* are larger than females and have large orange-red spots over the entire body and fins. These spots are also present in females, but they are smaller and less widely distributed. Males of *E. okaloosae* are slightly larger than females and both sexes lack red spots. The genital papilla of the breeding female is a low tube crowned with villi (Collette and Yerger, 1962, fig. 7).

The larger size of males, the absence of tubercles, and the shape of the genital papilla in females are three of the characters that differentiate *Villora* from the subgenus *Hololepis*, under which it has been synonymized by Bailey (*in* Bailey and Gosline, 1955). These characters help to substantiate my belief that *Villora* is an offshoot of the *asprigene–swaini* nontuberculate group of the subgenus *Oligocephalus* (Collette and Yerger, 1962, p. 214).

Subgenus *Austroperca* Hubbs

Males of *E. australe* Jordan, the only known species in this Mexican subgenus, taken on May 21 (UMMZ 136124, Chihuahua) and March 28 (UF 10127, Durango) have slightly enlarged testes and lack tubercles.

Subgenus *Psychromaster* Jordan and Evermann

No tubercles are present on the available material of *E. tuscumbia* Gilbert and Swain. Three males (USNM 125096, Alabama, Tennessee R., 36–38 mm.) which were apparently taken in the spring, although the date is unknown, have greatly enlarged testes and no tubercles. A 41 mm. female in this collection is filled with moderate-sized eggs. Males in a large collection taken on May 26 (UMMZ 104244, Alabama, Wheeler Reservoir) have the testes only slightly enlarged; the females are filled with large eggs.

The second species in this subgenus, *E. trisella* Bailey and Richards, is known only from the juvenile holotype.

Subgenus *Catonotus* Agassiz

This subgenus is composed of five described species: *flabellare* Rafinesque, *kennicotti* (Putnam), *obeyense* Kirsch, *squamiceps* Jordan, and *virgatum* (Jordan), plus several undescribed forms. All the species appear to be nontuberculate. The subgenus may, however, be divided into two species groups on the basis of another sexually dimorphic character. Both sexes of *E. kennicotti* and the males of *E. flabellare* and *E. squamiceps* have cream-colored, fleshy bulbs at the tips of the spines in the first dorsal fin. The tips of the dorsal spines in *flabellare*, and to a much lesser extent in *kennicotti*, are modified into a Y-shaped fork which supports the fleshy bulbs. These fleshy tips are essentially absent in both sexes of *E. obeyense* and *virgatum*, although small incipient bulbs are occasionally visible. Males of all species are darker than females, especially the pelvic, anal, and first dorsal fins, head, breast, and belly. Winn (1958b, p. 172) reported that males of *E. flabellare* were larger than females, had larger anal, pectoral, and pelvic fins, and lacked breeding tubercles. *E. flabellare* has a complex mating behavior which culminates in a pair spawning head to tail upside down underneath a rock (Lake, 1936, fig. 1; Winn, 1958a; 1958b, fig. 5).

Subgenus *Hololepis* Agassiz

This subgenus consists of six species: *serriferum* (Hubbs and Cannon); *gracile* (Girard); *zoniferum* (Hubbs and Cannon); *fusiforme* (Girard), with two subspecies; *saludae* (Hubbs and Cannon); and *collis* (Hubbs and Cannon), with two subspecies (Collette, 1962). Males of all species of *Hololepis* have tubercles on the anal rays and on the undersides of the pelvic fin rays. Males are generally darker than females, especially their dorsal, anal, and pelvic fins, and the venter. Females are larger than males or of about equal size. Males

of *E. gracile* and *E. zoniferum* have supplementary tubercles on the rami of the lower jaw and in life have vertical green bars on the sides and red spots on the first dorsal fin. Sexual dimorphism in these two species confirms their close relationships (Collette, 1962). Complete descriptions of coloration and breeding tubercles, photographs of sexually mature specimens, and drawings of breeding tubercles have been presented recently (Collette, 1962). Hubbs and Cannon (1935) reported tubercles in *E. serriferum*, *E. gracile*, and *E. fusiforme*.

The following account of tubercles in *Hololepis* is summarized from my recent revision (Collette, 1962). *E. serriferum* has tubercles most developed during late March, when they are present on the distal two-thirds of the anal fin rays and the distal third of the pelvic fin rays (Collette, 1962, p. 119 and fig. 1i). Hubbs and Cannon (1935) also found tubercles on the soft rays of the anal and pelvic fins of *E. serriferum*. Tubercles are present on *E. gracile* from February 19 (TNHC 4994, Texas, Red R.) to April 19 (KU 2418, Oklahoma, Red R.). Maximum development occurs in mid-March in Texas, when tubercles are present on the distal half of the anal rays, the distal three-fourths of the underside of the pelvic spine and rays, and in two rows of four tubercles on each ramus of the lower jaw (Collette, 1962 pp. 135–136 and figs. 1k, m). Hubbs and Cannon (1935) reported tubercles on the anal and pelvic fins and on the lower jaw of *E. gracile*. Cross (1954) also noted tubercles on the chin of this species. I found tubercles on only the anal rays and lower jaw rami of *E. zoniferum* (UMMZ 163758, Alabama, Tombigbee R.). I think they will be found on the pelvic rays also if sufficient material becomes available (Collette, 1962 p. 149–150). Tubercles are present on *E. saludae* from at least April 16 (CU 35019) until March 14 (CU 35036). At the maximum stage of development, tubercles are found on the distal three-fourths of the anal rays and on most of the ventral surface of the first four pelvic soft rays (op. cit., p. 191–192). In my limited material of *E. collis*, tubercles are developed on *E. c. collis* on March 22 (CU 11988) and on *E. c. lepidinion* Collette on March 31 (CU 29992). They are present on the underside of the pelvic fins and on most of the anal fin rays (op. cit., pp. 198, 205; fig. 1g).

There is geographic variation in tubercle development in *E. fusiforme*. Of thousands of specimens examined, tubercles were found on only a few specimens in 14 collections of the northern subspecies, *E. fusiforme fusiforme* (op. cit., p. 153), while they were commonly found on the southern *E. f. barratti* (op. cit., p. 175). Tubercles are present on *E. f. fusiforme* from March 25 (CU 29983, North Carolina, Ellis Lake) to May 17–18 (CU collections, New Jersey). They are present on *E. f. barratti* from October 27 (FSU 3273, Fla.) to May 29 (UG 516, South Carolina, Pee Dee R.) and are at their maximum de-

velopment from March 25 to May 29. Tubercles are present on more specimens for a longer period of time and are also better developed in the southern subspecies. I have found a similar type of geographic variation in *Percina* (*Percina*) *caprodes* and *Etheostoma* (*Oligocephalus*) *spectabile*. Egami (1954) also found a north–south difference in the development of dermal contact organs on the cyprinodontid *Oryzias latipes* (Temminck and Schlegel). Hubbs and Cannon (1935) found tubercles on the anal and pelvic fins of *E. f. barratti*, but only on the anal fin of *E. f. fusiforme*.

E. f. fusiforme is the only form that I have watched courting. The male mounts the female and "beats" her nape with the tuberculate undersides of his pelvic fins. At the same time, his tuberculate anal fin is in contact with the posterior part of her caudal peduncle. Thus the tubercles on the pelvic fins of males of *E. f. fusiforme* may serve to stimulate the female while the anal fin tubercles aid in maintaining contact. Fletcher (1957) has presented a photograph of a spawning pair.

The presence of breeding tubercles on the pelvic and anal fins of *Hololepis* and *Microperca*, and their absence from *Villora*, is one of the reasons I feel the first two subgenera are closely related to each other and not to *Villora* (Collette, 1962).

Subgenus *Microperca* Putnam

This most specialized subgenus of *Etheostoma*, contains three closely related species: *fonticola* (Jordan and Gilbert), *microperca* Jordan and Gilbert, and *proeliare* (Hay). Males of all three species have breeding tubercles on the anal rays and on the ventral surfaces of the pelvic fin rays as in the subgenus *Hololepis*. The fins of the males are all much darker than those of the females, especially the first dorsal, pelvic, and anal. Winn's description (1958b, p. 172) of the other sexually dimorphic features of *E. microperca* will serve equally well for the other two members of the subgenus: females larger than males; males with larger pectoral and pelvic fins; genital papillae of females elongate and tubelike; pelvic fins of males extremely long, with the outer ridge of thickened skin forming a cup (Petravicz, 1936, figs. 1, 2). The cuplike pelvic fins are furnished with tubercles which probably function in stimulation of the female or in maintenance of the spawning position (Petravicz, 1936, figs. 3, 4; Winn, 1958b, fig. 4).

Moderate sized conical tubercles are present on males of *E. fonticola* taken April 12 (USNM 166101, TU 4746, TU 5024, Texas, San Marcos R.). Tubercles are located on the distal tip of the first pelvic soft ray, on the entire length of pelvic soft rays 2–4, and on the distal

half of the last pelvic soft ray. Tubercles are also present on the distal seven-eighths of all elements of the anal fin.

Two males of *E. proeliare* (USNM 165959, Mississippi, Big Black R., April 8) have tubercles on all elements of the anal fin, on the tip of the first pelvic soft ray, and on the entire length of pelvic soft rays 2–5. Seventeen males (28–32 mm. standard length) from the Red River, Louisiana (USNM 172733), taken January 12, lack tubercles as do over 40 females. Seven other males in this collection (30–32 mm.) have tubercles on the distal half of pelvic soft ray 3 and a few scattered tubercles on the distal end of the second and fourth soft rays. Two males have a few tiny tubercles on the fourth anal ray. Thus, the tubercles seem to form first on the middle soft rays of the pelvic fin, spread to the other pelvic soft rays, and then develop on the anal fin rays.

Tubercles are present on males of *E. microperca* from as early as April 16 (UMMZ 81525, Michigan, Kalamazoo R.) until as late as July 10 (UMMZ 67927, Michigan, Big Wolf Cr.). They are absent on specimens taken from July 19 to December 21 (USNM), but few specimens are available from January through March. Tubercles develop first and remain for a longer period of time on the pelvic fin rays than on the anal fin rays. The maximum development I have observed is on males taken May 3 (UMMZ 73144 and 73158, Michigan, Au Sable R.). Tubercles are present on the entire length of the ventral surfaces of all the pelvic elements and on the anal spines. I have not seen specimens with tubercles developed on any of the anal soft rays as I have in the other two species of the subgenus. This poor development of tubercles is probably correlated with the northerly occurrence of *E. microperca*. A similar situation has also been shown in *Percina* (*Percina*) *caprodes*, *Etheostoma* (*Oligocephalus*) *spectabile*, and *E.* (*Hololepis*) *fusiforme fusiforme*. Petravicz (1936) failed to find tubercles on *E. microperca*, and Winn (1958b, p. 172) reported them on only the pelvic fins. *E. microperca* spawns in an approximately vertical position on plants. The male is mounted on the female's back with his tuberculate cuplike pelvic fins clasped over her back and his tuberculate anal fin in contact with her sides (Winn, 1958b, fig. 4).

Summary

Breeding tubercles are now known for 48 species in five genera of the Percidae. Tubercles in the Percidae are mainly distributed laterally and function primarily in facilitating contact between the male and female during the spawning act. Tubercles may have a stimulatory function, especially in the species that have them on the undersurface of the pelvic fins. Breeding tubercles are of value in classification at two levels.

First, they are present in the members of the tribe Etheostomatini, subfamily Percinae, and in the members of the tribe Romanichthyini, subfamily Luciopercinae. This fact might seem to suggest that the Romanichthyini and the Etheostomatini should be placed together, separate from the Percini and Luciopercini. When coupled with other characters, such as the reduction of the air bladder, the small body size, and the utilization of lotic rather than lentic habitats, this arrangement seems even more reasonable. However, as I have shown by using osteological characters (Collette, 1963), the relationships of the Etheostomatini are with the Percini, and those of the Romanichthyini are with the Luciopercini. Closer analysis of the distributions of tubercles confirms this. In the Etheostomatini, tubercles are concentrated on ventral and ventrolateral surfaces, such as the undersides of the pelvic fins, the anal fin, the lower part of the caudal fin, the scales on the belly, and the sides up to the lateral line. In the Romanichthyini, tubercles are concentrated on the dorsal and dorsolateral surfaces, the top of the head, the dorsal fins, the pectoral fin, and the body scales primarily above the lateral line. This difference in the distribution of tubercles may indicate a different mode of spawning in the two tribes. Unfortunately, there appears to be no information available about spawning in the members of the Romanichthyini. Breeding tubercles and other characteristics that are similar in the two tribes have probably arisen as independent adaptations to a bottom-dwelling mode of life in streams.

Within the Etheostomatini, patterns of tubercle development are useful in showing phylogenetic relationships. The character has no value at the generic level, at least if three large inclusive genera, *Percina*, *Ammocrypta*, and *Etheostoma*, are recognized. However, within each of the two larger genera (*Percina* and *Etheostoma*) tubercle patterns offer an additional character in defining subgenera and species groups within subgenera.

In *Percina*, there are five nontuberculate subgenera (*Hypohomus*, *Alvordius*, *Hadropterus*, *Swainia*, and *Cottogaster*), two tuberculate subgenera (*Percina* and *Imostoma*), and one heterogeneous subgenus (*Ericosma*). On the basis of this character, perhaps the tuberculate *P.* (*Ericosma*) *evides* is not as intimately related to the nontuberculate *P. crassa* and *P. palmaris* as previous workers have indicated.

Males of all four species in the subgenus *Ammocrypta* and the one species in the subgenus *Crystallaria*, genus *Ammocrypta*, are tuberculate. I think that the tubercle distributions in these species will be found to be virtually identical, although I have not yet seen tubercles on the anal fin of *A.* (*A.*) *pellucida* and I have found tubercles on the caudal fin of *A.* (*A.*) *clara* alone. Thus, tubercle patterns agree with other characters that lead to synonymizing *Crystallaria* with *Ammocrypta*, at least at the generic level.

The greatest problems in the classification of the Percidae lie in the largest genus, *Etheostoma*. Twelve subgenera were utilized by Bailey (*in* Bailey and Gosline, 1955) and one more recently has been recognized (Collette and Yerger, 1962).

The subgenus *Boleosoma* is composed of at least two groups: the nontuberculate *nigrum* group of five species and the tuberculate *stigmaeum* group of three species, although in some other characters, *chlorosomum* of the latter group tends to be somewhat intermediate between the two. The nontuberculate monotypic subgenus *Ioa* clearly seems to be derived from the nontuberculate *nigrum* group. Further study may lead to synonymizing *Ioa* under *Boleosoma*, and removing *E. stigmaeum*, *E. jessiae*, and *E. chlorosomum* from *Boleosoma* and placing them in *Vaillantia* Jordan. Similarities in spawning behavior between *Ioa* and the *nigrum* group in contrast to the *stigmaeum* group reinforce this idea.

The subgenus *Etheostoma* can be divided into two closely related tuberculate groups and one nontuberculate group. The *variatum* group of five species is the only one in the Etheostomatini where both sexes are tuberculate. Other authors have previously pointed out the close relations which members of the *variatum* group have to one another. The *inscriptum* group of five species differs from the *variatum* group in that only the males develop tubercles. Four of the remaining five species (*rupestre*, *histrio*, *zonale*, and *blennius*) presently placed in the subgenus form a closely related nontuberculate group. This group appears to be somewhat intermediate between the *variatum* and *inscriptum* groups on the one hand and the nontuberculate subgenus *Ulocentra* on the other. It will be necessary to await the description of some nine new species of *Ulocentra* presently in manuscript by Reeve M. Bailey before a full appraisal can be made of the relations between the *zonale* group and *Ulocentra*. The two type specimens of *E. sellare* are females caught in the spring; they are not tuberculate. Therefore, it probably should not be placed in the *variatum* group, although a number of authors have indicated that its relationships are with that group. *E. sellare* does not appear to be close to either the *inscriptum* or *zonale* groups and I am not satisfied that it belongs in the subgenus *Etheostoma*.

The monotypic subgenera *Allohistium* and *Austroperca* are apparently nontuberculate. *Psychromaster* is also apparently nontuberculate. The lack of tubercles in all species of *Nothonotus* and *Catonotus* further indicates the compact nature of each of these subgenera.

The largest subgenus, *Oligocephalus*, contains about 20 species which belong in at least four species groups. The three forms of the *nianguae* group are very closely related to each other as was noted by Bailey (1948) and Kuehne and Bailey (1961). The *radiosum* group is similar to the *nianguae* group in having tubercles on the body scales,

but this may not be an indication of close relationship. The *spectabile* group consists of nine species, all of which have tubercles on the anal fins of males. All but *E. parvipinne* and *E. fricksium* of this group have tubercles on the ventral scales and the pelvic fins. *E. punctulatum*, *E. luteovinctum*, and *E. spectabile* also have additional tubercles on the lower part of the caudal fin and *E. spectabile* even has tubercles on the pectoral fin. Probably most of the remaining eight species are nontuberculate.

Both species of the subgenus *Villora* lack breeding tubercles, further indicating that *Villora* is probably an offshoot of the nontuberculate group of *Oligocephalus*, perhaps from somewhere near *E. swaini* and *E. asprigene*, and consequently it was removed from synonymy with *Hololepis* (Collette and Yerger, 1962).

The presence of breeding tubercles on the anal and pelvic fins of the species in the subgenus *Hololepis* shows its close relationships with the subgenus *Microperca* and not with *Villora* (Collette, 1962). The presence of tubercles on the chin of *E. gracile* and *E. zoniferum* confirms other evidence that these two species of *Hololepis* are especially closely related (Collette, 1962).

Thus, the patterns of breeding tubercles confirm the close relationships within many subgenera and species groups of the Percidae and indicate that several other groups may need rearranging.

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